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Recovery potential assessment of 4T and 4VW winter skate (*Leucoraja ocellata*): Population models.

Évaluation du potentiel de rétablissement de la raie tachetée (*Leucoraja ocellata*) de 4T et 4VW : modèles de population

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ABSTRACT

In May 2005, winter skate (*Leucoraja ocellata*) in the southern Gulf of St. Lawrence (sGSL, NAFO Div. 4T) and on the eastern Scotian Shelf (eSS, Div. 4VW) were designated as endangered and threatened, respectively, by the Committee on the Status of Endangered Wildlife in Canada. In this report, we model the population dynamics of 4T and 4VW winter skate using Bayesian state-space models. Data inputs were 35-yr time series of research survey catch rates for juvenile and adult length classes in each area, and estimates of fishery landings and bycatch. The models suggested that there have been changes in the mortality of winter skate, with juvenile mortality decreasing and adult mortality increasing from the 1970s to the 1980s and 1990s. Similar patterns were evident in both the 4T and 4VW areas, though the patterns were stronger in 4T. These changes in mortality appeared to reflect changes in natural mortality (*M*). For adults in the 4T area, the trend in exploitation rate was opposite to the trend in total mortality, and the estimated exploitation rate was very low after 1990. Possible causes of the trends in *M* were examined by modeling *M* as a function of potential explanatory variables such as predator abundance. In both the 4T and 4VW areas, adult *M* showed a significant positive relationship with grey seal abundance, suggesting that increased predation by seals may be a cause of the increased adult mortality. Population projections predicted a steady decline in the 4T population even in the absence of fishery removals. For the 4VW population, projections predicted a continued decline at recent (2002-2004) levels of removals, and a reduced decline or stability if there are no removals. These projections suggest that no recovery can be expected for either population at the current levels of adult natural mortality. Uncertainty around the projections was high, but in the case of the 4T population the 95% credible limits around the projected abundance over the next 10 years did not include recovery.

RÉSUMÉ

En mai 2005, le Comité sur la situation des espèces en péril au Canada (COSEPAC) a désigné la population de la raie tachetée (Leucoraja ocellata) du sud du golfe du Saint-Laurent (SGSL, div. 4T de l'OPANO) et celle de l'est du plateau néo-écossais (EPNE, div. 4VW) comme étant en voie de disparition et menacée respectivement. Dans le présent rapport, nous modélisons la dynamique des populations de raie tachetée des divisions 4T et 4VW au moyen de modèles bayésiens de type état-espace. Les données utilisées sont, d'une part, les taux de prises pour les classes juvéniles et adultes (série chronologique de 35 ans) d'après les relevés de recherche menés dans chaque zone et, d'autre part, les estimations des débarquements et des prises accessoires de la pêche. Les modèles montrent qu'il y a eu des changements dans la mortalité de la raie tachetée; la mortalité chez les juvéniles ayant diminué et la mortalité chez les adultes ayant augmenté à partir des années 1970 jusqu'aux années 1980 et 1990. On observe des changements semblables dans les divisions 4T et 4VW, bien qu'ils soient plus prononcés dans la division 4T. Ces changements dans la mortalité semblent refléter les changements dans la mortalité naturelle (M). Chez les adultes de la division 4T, la tendance relative aux taux d'exploitation s'oppose à la tendance relative à la mortalité totale, et le taux d'exploitation estimé est très faible après 1990. Pour établir les causes possibles des tendances relatives à la mortalité naturelle, on a modélisé M en fonction de variables explicatives possibles telles que l'abondance des prédateurs. Chez les adultes des divisions 4T et 4VW, il existe une relation positive significative entre la mortalité naturelle et l'abondance des phoques gris, ce qui suggère que la prédation accrue par les phoques pourrait être à l'origine de la mortalité accrue chez les raies adultes. D'après les projections démographiques, l'abondance de la population de la division 4T continuera à diminuer de façon constante même en l'absence des prélèvements de la pêche. Selon les projections pour la population de la division 4VW, on observera un déclin continu si les niveaux actuels de prélèvements (2002-2004) sont maintenus, et un déclin moindre ou une stabilité s'il n'y a aucun prélèvement. Ces projections laissent croire qu'aucun rétablissement n'est possible pour l'une ou l'autre des populations aux niveaux de mortalité naturelle actuels des adultes. L'incertitude entourant ces projections est grande, mais dans le cas de la population de la division 4T, les limites plausibles de 95 % concernant l'abondance prévue pour les dix prochaines années n'incluent pas le rétablissement.

INTRODUCTION

Winter skate (*Leucoraja ocellata*, Family Rajidae) are endemic to the Northwest Atlantic, occurring from Cape Hatteras to the northern Gulf of St. Lawrence and southern Newfoundland. In May 2005, the status of winter skate was considered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Four designatable units (DUs) were identified. The southern Gulf of St. Lawrence (NAFO[1] Division 4T) DU was designated as Endangered (EN) while that of the eastern Scotian Shelf (NAFO Div. 4VW) was designated as Threatened (TH). The two other DUs (Georges Bank/Bay of Fundy/Western Scotian Shelf, 4X5Ze and Newfoundland/ northern Gulf of St. Lawrence, 3PnNO4RS) were designated as Special Concern and Data Deficient respectively. These DUs are being considered for listing in Schedule 1 of the Canada's Species at Risk Act (SARA). If listed under SARA as EN or TH, activities that would harm the species would be prohibited and a recovery plan would be required. Before the listing decision is made, decisions on permitting incidental harm and in support of recovery planning need to be made.

A companion document (Swain et al. 2006) describes the biology and evaluates the current status of winter skate in the southern Gulf of St. Lawrence (sGSL, 4T) and on the eastern Scotian Shelf (eSS, 4VW). Potential sources of mortality/harm are also documented in Swain et al. (2006). Benoît (2006) gives estimates of fishery bycatch of winter skate in the southern Gulf.

In this document, we model the population dynamics of 4T and 4VW winter skate using Bayesian state-space models. Data inputs and information used to determine the priors for these models are described in detail in Swain et al. (2006). These models are used to evaluate causal factors in the changes in abundance of winter skate since the early 1970s and to examine the recovery potential of winter skate in 4T and 4VW, to the extent possible given the limited data available on these populations.

METHODS

We used Bayesian state-space models, implemented using WinBUGS, to investigate patterns in mortality in these populations. These models consist of two coupled components, a state process model and an observation model. The first model represents the unobservable stochastic processes governing the population's dynamics. The second model describes the observation errors (Fig. 1).

Because age-disaggregated data were not available for these populations, we used stage-structured population models (Fig. 1). These models consisted of one or two juvenile stages and an adult stage. Individuals moved from the juvenile

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stage to the adult stage (or from the first juvenile stage to the second juvenile stage) based on a transition probability, θ. Individuals in stage *i* survived from time *t* to time *t*+1 with probability $\exp(-Z_i)$. The number of individuals recruiting to the (first) juvenile stage equaled the number of adults at time *t-a* times a recruitment rate *r*/2 (half the adults were assumed to be female), where *a* is the youngest age in the juvenile stage and *r* equals the annual fecundity discounted by egg case mortality and juvenile mortality up to age *a*. Demographic and environmental stochasticity was introduced via independent and identically distributed log-normal errors with mean 0 and variance σ^2_i. The observation series was provided by the mean catch rates in annual bottom-trawl surveys, grouped into stages based on length. These were related to the unobserved abundances of each stage *i* by catchability q_i and log-normal observation error.

This model is unrealistic in one important respect. Juveniles move to the adult stage with probability θ instead of ageing within the juvenile stage and moving to the adult stage at the age of maturity. We explored models with age structure in the juvenile stage (i.e., recruits could not move to the adult stage until they had remained in the juvenile stage for a number of years). However, sampling was impractically slow with these models.

Because the stage-structured survey indices contained limited information for estimating population dynamics parameters, we provided informative priors where possible and focused on estimating mortality parameters.

Southern Gulf (4T) Model

Winter skate in the sGSL appear to be distinct from those elsewhere (McEachran and Martin 1977). They mature at a smaller size and have a smaller maximum size than do winter skate in other areas. Outside of the sGSL, winter skate are sympatric with a closely related species, the little skate *L. erinacea*. McEachran and Martin (1977) suggest that these differences between winter skate inside and outside of the sGSL reflect character displacement between little and winter skate in areas of sympatry. Because winter skate in the sGSL resemble little skate in size at maturity and maximum size, our priors for sGSL winter skate are sometimes based on life history information for little skate rather than information for the very different winter skate populations outside of the sGSL.

This model had two stages: a juvenile stage comprised of skates 21-41 cm in length, and an adult stage comprised of skates 42 cm or longer. Based on published growth rates of winter and little skate (Swain et al. 2006, Table 1), individuals were assumed to enter the juvenile stage one year after hatching. Priors for the basic model are given in Table 1. A moderately informative prior was provided for recruitment rate *r*, centered on 7.5. This was obtained assuming an average annual fecundity of 30 (from Frisk et al. 2002, for little skate), a survival rate of 75% for egg cases (Lucifora and Garcia 2004), and a survival rate of 33% during the year between hatching and recruitment to the

juvenile stage. An incubation period of 1 year within the egg case was assumed, a compromise between the 6-9 months reported for little skate and the 18-22 month reported for winter skate, taking into account the warm temperatures that would be experienced in shallow inshore areas in summer. Thus, recruitment depended on adult abundance in year t-2. Uniform priors were used for mortality parameters (e.g., Table 1).

The data contained no information for estimating θ (i.e., given a uniform prior, the estimated posterior was also uniform). In winter skate populations maturing at about 75 cm, mean lengths near 42 cm are reached by age 4 yr (42.2 cm, Frisk 2004) or 5 yr (44.9 cm, Sulikowski et al. 2003). In little skate maturing at about 43-46 cm, a mean length near 42 cm is reached by age 6 yr (42.9 cm, Frisk 2004). We assumed that winter skate in the sGSL, which mature at about 42 cm, reach this length at an age of about 6 yr. This suggests a duration of 5 yr for the juvenile stage, implying θ=0.2. Our prior for θ peaked at 0.2 and was restricted to the range 0.15-0.25.

Priors for the initial population sizes (adults in 1969 and 1970, and juveniles in 1970) were based on the average survey catch rates in the early to mid 1970s, and were highly informative (Table 1). No attempt was made to estimate catchability to the survey. In models that included fishery removals, survey abundance indices were scaled to absolute abundance (Swain et al. 2006, Appendix B) prior to input as data. Thus q was given a strongly informative prior centered on 1. The exception was q for juveniles in models without fishery removals. In this case, the survey indices were used as indices of relative abundance and the difference between juveniles and adults in availability within the survey had to be taken into account (Swain et al. 2006, Appendix E). This difference in availability suggested a prior centered on 0.7 for juvenile q when adult q was centered on 1. (In the models with fishery removals, this difference in availability was taken into account when the survey indices were scaled to absolute abundance prior to input as data (Swain et al. 2006, Appendix B).)

Vague priors were used for process error (uniform for process SD, Table 1). We set limits for the priors for observation error based on the CV of the survey data. The CV was near 0.4. We used this as a lower limit for the prior and set the upper limit at double this value. Initial trials suggested that this range was too low for the juvenile observation error, and we adjusted its prior accordingly (Table 1).

Data inputs were the abundance indices from the annual September bottom-trawl survey of the sGSL (see Swain et al. 2006 for details), and in some cases the median estimates of discards for juveniles and adults (Benoit 2006, Swain et al. 2006). In models without fishery removals, the survey catch rates were adjusted for size selectivity using the flatfish (plaice) curve estimated by Harley and Myers (2001). We set γ to 1 (i.e., at this stage, we attempted to adjust small and large individuals to the same relative catchability, but not to 100% catchability). In models with fishery removals, we attempted to scale the indices to absolute

abundance by attempting to 1) fully adjust for catchability, 2) adjust for availability, and 3) expand from swept area to survey area (Swain et al. 2006, Appendix B).

These scaled indices were based on the standard day-adjusted time series (Swain et al. 2006). Adjustment for diel differences in catchability was necessary because fishing in the September survey was during daytime only in 1971 – 1983 but throughout the entire 24-hr day since then. Catchability of winter skate to the survey is greater at night than in daytime, and the diel difference in catchability is greater for smaller skates (Benoît and Swain 2003). Thus, the adjustment for diel differences in catchability affects the ratio of juveniles to adults in the input data. This will affect model estimates of mortality rates but should not affect estimates of trends in these rates.

Three classes of models were examined:

1) *Z* models: In these models, we attempted to estimate total mortality of juveniles and adults, and test for trends in total mortality. An example of one of these models is given in Appendix A. Refer to this model for basic process and observation equations.
2) *M* models: These models included discards as fishery removals. Based on the information in Benoît (2006), we used an informative prior for the discard survival rate, peaking at 0.3 (Beta(30,70)). In these models, we attempted to estimate natural mortality of juveniles and adults, and test for trends in natural mortality. An example of one of these models is given in Appendix B. Refer to this model for basic process and observation equations.
3) *M*-covariate models: These models were similar to the *M* models in that they included discarded removals. However, instead of modeling *M* as constant or as a time trend, *M* was modeled as a function of potential explanatory factors (i.e., seal abundance, large-cod abundance, or environmental conditions).

Eastern Scotian Shelf (4VW) Model

This model had three stages: (1) an adult stage comprised of skates 75 cm and longer, (2) a juvenile stage comprised of skates 60-74 cm in length, corresponding to juveniles that are caught at a relatively high rate in the directed skate fishery, and (3) a juvenile stage comprised of skates 36-59 cm in length, corresponding to juveniles caught at a low rate in the directed skate fishery. Based on growth models reported by Sulikowski et al. (2003) and Frisk (2004) (Table 1), skates were assumed to recruit to the first juvenile stage at an age of 3 yr, move to the second juvenile stage at an age of 8 yr, and mature to the adult stage at an age of 12 yr. This suggests values of 0.2 for θ_1 (transition probability between juvenile stages) and 0.25 for θ_2 (transition probability from the second juvenile stage to the adult stage).

Annual fecundity was assumed to be 35 egg cases (Frisk et al. 2002). Incubation period within egg cases was assumed to be 2 yr (J.E. Simon, unpublished data; Sulikoswki et al. 2003). Egg case mortality was assumed to be 25% per year (Lucifora and Garcia 2004). These assumptions suggested a recruitment rate to hatching (r) of 20 skates per spawning female. Survival over the first 3 yr (s.prerec) was assumed to be about 6% ($0.35 \times 0.40 \times 0.45$). Recruitment to the first juvenile stage was assumed to equal adult abundance in year t-5 times $r/2$ times s.prerec.

Informative priors were provided for initial population sizes and catchability, as described above for the 4T model. Unlike in the 4T model, no difference in availability within the survey area was assumed between juveniles and adults. Limits for the priors for observation error were initially based on the CV of the survey data. However, initial runs indicated that the upper limits were to low, and these were raised. Vague (uniform) priors were used for process error and mortality parameters. Priors are listed in Table 2.

Data inputs were the survey abundance indices, and in some cases estimated numbers landed and discarded for each of the model stages. In models without removals, the abundance indices were relative indices, but were adjusted for size selectivity as described above for the 4T model. In models with removals, we attempted to scale the survey indices to the level of absolute abundance prior to input as data.

Models were of the general types described above for the 4T case.

RESULTS AND DISCUSSION

Southern Gulf (4T)

Z models

Three models were examined, termed here as Zbar, Zdec, and Ztrend. In Zbar, juvenile and adult mortality were assumed to be constant over the time series. Z was estimated to be about 1.3 for juveniles and 0.35 for adults (Fig. 2). This model did not fit the juvenile abundance trend well, tending to overestimate juvenile abundance early in the time series and underestimate it for the remainder of the time series (Fig. 2). This model also tended to underestimate adult abundance early in the time series (Fig. 2).

In Zdec, decadal variation in mortality was allowed. This model fit the trends in both juvenile and adult abundance well (Fig. 3). Estimated juvenile Z decreased from about 2.5 in the 1970s to about 1.0 in the 1980s and the 1990s/2000s (Fig. 3). Estimated adult Z increased from a value near 0.1 in the 1970s to values near 0.5 in the 1980s and 0.6 in the 1990s/2000s (Fig. 3).

In Ztrend, mortality was modeled as trends over time. Results of one version of this model, with adult mortality modeled as a linear trend and juvenile mortality modeled as a quadratic trend, are shown in Figure 4. Results for other forms of trend are shown in Appendix C. All versions of this model indicated an increase in adult mortality and a decrease in juvenile mortality over time. The increase in adult mortality appeared to be roughly linear. For example, in the quadratic model, the parameter for the quadratic term did not differ from zero for the adult Z trend (Appendix C). Similarly, in the asymptotic model, the adult Z trend did not depart strongly from a linear trend (Appendix C). On the other hand, the decline in juvenile mortality appeared to be non-linear, with juvenile Z declining early in the time series and then leveling off. All the Ztrend models fit the trends in both juvenile and adult abundance well (e.g., Fig. 4).

Based on DIC (Deviance Information Criterion), all models allowing temporal variation in mortality were a substantial improvement over the model with constant mortality (Table 3). The best model was the Ztrend model with a linear trend in adult mortality and a quadratic trend in juvenile mortality, followed by the Zdec model. However, the Zdec model and all the Ztrend models fit the data about equally well.

The very low juvenile abundance indices at the start of the time series are suspicious. The same very low abundance indices for juveniles are evident in the 4VW area at the start of the time series in that area. Very different sizes of skate are involved in the two cases. At the start of the 4T series, skates over 40 cm were abundant while those below this length were rare. At the start of the 4VW series, skates over 80 cm were abundant while those below this length were rare. Length distributions in survey catches in both areas in the 1960s were also similar to those observed at the start of our time series (McEachran and Martin 1977). We know of no changes in survey methods or gear that would bias these early catch rates relative to subsequent ones. Nonetheless, we investigated the sensitivity of our results to these low juvenile indices at the start of the time series. We ran the Zdec model setting the first 3 juvenile data points to missing. This had a negligible effect on the estimated trends in both juvenile and adult mortality, indicating that these trends were not strongly influenced by these early data points.

M models

These models decomposed total mortality into fishing mortality and natural mortality. Fishing mortality depended on estimated discards and the discard survival rate. We used an informative prior for the discard survival rate, peaking at 0.3, and the posterior was little changed from this prior (Fig. 5).

Model Mdec allowed decadal variation in natural mortality. This model fit the data as well or better than Zdec (Figs. 3 and 6). Based on this model, the exploitation

rate on adults was highest at the start of the time series and declined throughout the 1970s and early 1980s (Fig. 7). Estimated exploitation rate was very low for adults after 1990 and for juveniles over the entire time series. For adults, the trend in exploitation rate was opposite to the trend in total mortality, indicating that the increase in adult mortality after the 1970s was due to an increase in natural mortality (or unknown human-induced mortality that is interpreted as natural mortality in the models). Estimated decadal variation in *M* was similar to the variation in *Z* except that the trend in adult *M* (Fig. 6) was stronger than the trend in *Z* (Fig. 3), reflecting the opposing directions of trends in exploitation rate and *M* for adults. For juveniles, estimates of *M* for each decade were very similar to the estimates of *Z*, reflecting the very low exploitation rate on juveniles.

Results were similar for the Mtrend model (quadratic trend for juveniles, linear trend for adults). Again, this model fit the data as well or better than the corresponding Ztrend model (Figs. 4 and 8). A linear trend in adult *M* was indicated, with a slope similar to the linear trend in adult *Z* in the corresponding Ztrend model. The quadratic trend in juvenile *M* was very similar to the corresponding trend in Z, again reflecting the very low exploitation rate estimated for juveniles.

M-covariate models

We tested the following hypotheses:

1. Trends in adult *M* reflect changes in predation by seals
2. Trends in juvenile *M* reflect changes in predation by seals and/or cod
3. Trends in juvenile and/or adult *M* reflect changes in environmental conditions

Covariates were the indices of seal abundance, large cod abundance, and inshore temperatures. Predator abundance indices were transformed by subtracting their minimum and dividing by their SD. A positive relationship between *M* and predator abundance was expected for direct effects of predation. No particular direction was expected *a priori* for relationships between *M* and environmental conditions.

Adult *M* showed a strong positive relationship with the index of grey seal abundance (Figs. 9-11). The relationship was highly significant, with less than 0.00025 of the posterior density of the slope parameter for the effect of seals below zero (Fig. 9).

For juveniles, the relationship between *M* and seal abundance was weaker and not in the expected positive direction (Fig. 9), suggesting that this relationship is spurious or reflects an indirect effect due to predation on predators or competitors of juvenile skates. In a model with adult M a function of seal abundance and juvenile M a function of the abundance of large cod (Fig. 10), the effect of cod abundance was in the expected positive direction but was not

significant. The effect of cod abundance remained non-significant including seal abundance as a second covariate of juvenile *M* (Fig. 11); in this case, neither the effect of cod abundance or seal abundance on juvenile *M* was in the expected direction.

With *M* modeled as a function of temperature, adult *M* was unrelated to the temperature index, while juvenile *M* showed a significant inverse relationship to temperature (Fig. 12).

Projections

In order to evaluate recovery potential, winter skate abundance was projected 10 years into the future using the state-space models. Projections were based on the model with decadal variation in *M*. Future *M* was assumed to be at the 1990-2004 level. Future bycatch was assumed to be a) nil, b) at the 2002-2004 level (about 10 t), or c) at the 1993-2001 level (about 50 t). Based on these projections, the population is expected to steadily decline even in the absence of any bycatch in fisheries (Fig. 13). Bycatch at the most recent (2002-2004) level has a negligible effect on the rate of decline. However, slightly higher bycatch, at the 1993-2001 level, sharply accelerates the expected rate of decline. The uncertainty around the 10-year projection is large but does not include recovery.

Conclusions

These models suggest that adult mortality increased and juvenile mortality decreased during the 1971-2004 period. For juveniles, the decline in mortality appeared to occur in the 1970s, with mortality relatively constant since then. For adults, the increase in mortality may have occurred mainly in the 1980s with little further increase in the 1990s, or the increase may be on-going. The trend in adult mortality appears to be unrelated to direct effects of fishing. The exploitation rate on adults due to discarded bycatch appeared to decline over the time series (Fig. 7) as adult mortality increased. Taking estimated discards into account, the trends in adult natural mortality were very similar to the trends in total mortality of adults.

Adult *M* showed a significant positive relationship with grey seal abundance, suggesting that increased predation by seals may be a cause of the increased adult mortality. However, seal predation is thought to be focused on small fish, whereas juvenile *M* and seal abundance were not positively related. In mass-balance models of the sGSL ecosystem, total consumption by predatory fishes was about ten times that by marine mammals in the mid-1980s (Savenkoff et al., in press). Possibly, any increased predation by seals on juvenile skate has been offset by reduced mortality from predation by large demersal fishes, which declined in abundance in the 1980s and 1990s. The models that included both large cod abundance and seal abundance as covariates of juvenile *M* did not support this suggestion, though such trade-offs in effects may be difficult to

detect through correlation analyses. Alternatively, improving environmental conditions (suggested by the inverse relationship between inshore temperature and juvenile M) may have offset effects of increased seal predation on juveniles.

A final caveat is that not all potential threats could be included in these population models. For example, the scallop fishery in the southern Gulf represents potential source of winter skate bycatch mortality, but the magnitude of bycatch in this fishery is unknown (Swain et al., 2006) and thus could not be included in the bycatch estimates used in our models.

While the causes of the apparent increase in the natural mortality of adults are uncertain, our models suggest that both juvenile and adult abundance will continue to decline in the near future, even in the absence of bycatch in fisheries for demersal fishes and shrimp.

Eastern Scotian Shelf (4VW) Model

Z models

In the Zbar model, mortality was assumed to be constant over the time series for each stage. The model fit the trends in abundance indices well, except for a tendency to overestimate juvenile abundance early in the time series, particularly for the first juvenile stage (Fig. 14). Posterior medians for Z were 0.25 for the first juvenile stage, 0.48 for the second juvenile stage and 0.22 for the adult stage.

In the Zdec model, decadal variation in mortality was allowed. Model fit was similar to that for the Zbar model (Fig. 15). For the first juvenile stage, the posterior median for Z was higher for the 1970s (0.67) than for the 1980s and 1990s (0.28 and 0.25, respectively), but the posteriors for Z in the three decades overlapped broadly. For the second juvenile stage, posteriors again suggested somewhat higher Z in the 1970s (median 0.59) than in later decades (medians 0.40 and 0.46), but the differences were slight and overlap among the posteriors broad. For adults, Z appeared to increase progressively over the time series, with posterior medians of 0.11 for the 1970s, 0.22 for the 1980s and 0.41 for the 1990s/2000s. In this case, there was less overlap between the posteriors for Z in the 1970s and 1990s.

We fit several Z-trend models. These provided little support for a trend in Z for juvenile stage 2 but provided some support for a quadratic trend in Z for juvenile stage 1 and a linear trend for adults. Results for a model with these trends in Z are shown in Figure 16. Both slope parameters for the quadratic trend in Z for juvenile stage 1 differed significantly from zero. The fitted relationship suggested declining Z in the 1970s for this stage. The slope parameter for the linear trend in

adult Z was also (marginally) significant, suggesting increasing adult Z over the 1970-2004 period.

These models suggest trends in Z for winter skate in 4VW that are generally similar to those seen in 4T. Z appeared to decrease for stage-1 juveniles in the 1970s and, in contrast to the juvenile trend, progressively increase for adults over the time series. However, the evidence for changes in Z in 4VW was not as strong as that in 4T. Fit to the data was similar for all the Z models, though DIC was somewhat lower (indicating a better model) for the "hybrid" trend model in Figure 16 (DIC=340.0) than for the Zbar (345.9) and Zdec (348.6) models.

M models

These models decomposed total mortality into fishing mortality and natural mortality. Fishing mortality depended on landings, estimated discards and the discard survival rate. We used an informative prior for the discard survival rate, peaking at 0.3. Similar to the 4T models, the data contained no information suggesting a different value for discard survival, with the posterior very similar to the prior (Fig. 17).

In the Mbar model (Fig. 18), posterior medians for M were 0.18 for juvenile stage 1, 0.34 for juvenile stage 2 and 0.14 for the adult stage. Comparing with the Zbar model, this suggests fishing mortality (F) near 0.1. The Mdec model suggested trends in M similar to the trends in Z (Fig. 19). For juvenile stage 1, M appeared to decrease from the 1970s to the 1980s and then level off (posterior medians for M: 0.66 in the 1970s, 0.23 in the 1980s and 0.23 in the 1990s). However, overlap between the posterior medians for M was broad between decades for this stage. For juvenile stage 2, M appeared to vary little over time (posterior medians for M: 0.39 in the 1970s, 0.30 in the 1980s and 0.36 in the 1990s). For adults, M appeared to increase steadily over time (posterior medians for M: 0.06 in the 1970s, 0.13 in the 1980s and 0.31 in the 1990s). As for Z, overlap between the posteriors for M was relatively slight for adults between the 1970s and 1990s (though the overlap was greater for M than for Z).

Results for an M-trend model, with a quadratic trend in M for juvenile stage 1, constant M for juvenile stage 2 and a linear trend for adults, are shown in Figure 20. Both slope parameters were significant for the juvenile-1 trend; the fitted trend suggested that M for this stage declined in the 1970s. The increasing linear trend in adults M was marginally significant. A similar model, but with adult mortality a function of seal abundance, is shown in Figure 21. The slope parameter for the effect of seal abundance is marginally significant.

Fit to the data was similar for all the M models, though DIC was somewhat lower (indicating a better model) for the "hybrid" trend model in Figure 20 (DIC=873.3) and the "seal" model in Figure 21 (DIC=874.9) than for the Mbar (878.4) and Mdec (881.1) models.

Based on the *M* models, the exploitation rate on all size classes declined in the early 1990s (Figure 22), when fishing effort in groundfisheries declined sharply. Estimated exploitation rate on the larger skates (60+ cm) increased with the start of the directed skate fishery in 1994, but declined in the late 1990s as catches in this fishery were reduced. The estimated exploitation rate on all size classes has been very low in recent years.

Projections

The population model was used to project population abundance over the next 10 years to evaluate recovery potential. Projections were based on the model with decadal variation in *M*. Future *M* was assumed to be at the 1990-2004 level. Future fishery removals were assumed to be either nil or at the 2000-2004 level (about 230t landed and 70t discarded). Bycatch in the scallop fishery is unknown and could not be incorporated in the models. The model predicts a continued decline in abundance at current levels of removal and a reduced decline or stability if removals are set at zero (Fig. 23). However, the uncertainty about the projection was great and encompassed both extirpation and recovery in the 95% credible limits around the median trend. Based on the most probable trend, no recovery is expected without a decrease in adult natural mortality (or unknown human-induced mortality that is interpreted as natural mortality in the models).

Projections with the Mbar model were slightly more optimistic. Adult abundance is constant if fishery removals are kept to zero but slowly declines if fishery removals are kept at the current low level. Juvenile abundance is roughly constant in either scenario (after an initial decline for the larger juveniles).

In projections with the "hybrid" M-trend model, declines were more severe, as expected given the projection in adult M to even higher levels in the future. In this case, steep declines in abundance occurred for all stages even in the absence of fishery removals. With fishery removals held at the current low level, extinction occurred in less than 10 years.

Conclusions

These models suggest that the exploitation rate on 4VW winter skate was about 0.05-0.10 in the 1970s and 1980s. The exploitation rate declined on all size classes in the early 1990s as groundfishing effort declined, but increased on larger skates with the start of the directed skate fishery in 1994. As catches in this fishery were reduced, the exploitation rate declined to very low levels for all size classes in recent years.

These models suggest trends in mortality similar to those indicated for winter skate in the sGSL, with juvenile mortality decreasing from the 1970s to the 1980s and adult mortality progressively increasing over the 1971-2004 period. However,

the evidence for these changes in mortality were not as strong as in the sGSL population.

Changes in mortality of 4VW winter skate appeared to mainly reflect changes in natural mortality. The estimated increase in natural mortality of adults coincided with increases in the abundance of grey seals in the 4VW area. However, it is possible that the apparent changes in natural mortality may reflect unknown human-induced mortality not incorporated in the models (e.g., bycatch in scallop fisheries).

Model projections suggest continued population declines at recent (2002-2004) levels of fishery removals, and a reduced decline or stability if removals are set to zero. However, uncertainty around these projections is high.

ACKNOWLEDGEMENTS

We thank Jim Simon for information on winter skate biology.

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Table 1. Prior probability density functions (PDFs) on parameters for the basic 4T model.

Parameter	Prior
Z.j	~Uniform(0,5)
Z.a	~Uniform(0,3)
r	~Normal(7.5,0.1)|(0,)[1]
θ	~Beta(20,80)|(0.15,0.25)
SDobs.j	~Uniform(0.6,1.2)
SDobs.a	~Uniform(0.4,0.8)
SDpro.j	~Uniform(0,1)
SDpro.a	~Uniform(0,1)
N69.a	~Normal(0.4,100)|(0,)
N70.a	~Normal(0.4,100)|(0,)
N70.j	~Normal(0.1,10)|(0,)
q.j	~Normal(0.7,100)|(0,)
q.a	~Normal(1,100)|(0,)

[1]Note that the second parameter of the Normal distribution is given as precision ($1/\sigma^2$) in this table.

Table 2. Priors on parameters for the basic 4VW model.

Parameter	Prior
Z.j1	~Uniform(0,3)
Z.j2	~Uniform(0,3)
Z.a	~Uniform(0,3)
R	~Normal(20,10)I(0,)[1]
s.prerec	~Beta(6.3, 93.7)
θ_1	~Beta(20,80)
θ_2	~Beta(25,75)
SDobs.j1, SDobs.j2	~Uniform(0.6, 2)
SDobs.a	~Uniform(0.4,1.8)
SDpro.j1, SDpro.j1, SDpro.a	~Uniform(0,5)
N.a[1965:1969]	~Normal(3.0,100)I(0,)
N69.j1	~Normal(3.5,100)I(0,)
N69.j2	~Normal(1.0,100)I(0,)
q.j1, q.j2, q.a	~Normal(1,100)I(0,)

[1]Note that the second parameter of the Normal distribution is given as precision ($1/\sigma^2$) in this table.

Table 3. DICs (Deviance Information Criteria) for the sGSL Z models.

Model	DIC
Zbar	-135.77
Zdec	-157.46
Ztrend – both linear	-156.63
Ztrend – both quadratic	-156.59
Ztrend – both asymptotic	-155.73
Ztrend – both sigmoid	-155.94
Ztrend – juvenile quadratic, adult linear	-158.29
Ztrend – juvenile asymptotic, adult linear	-156.40

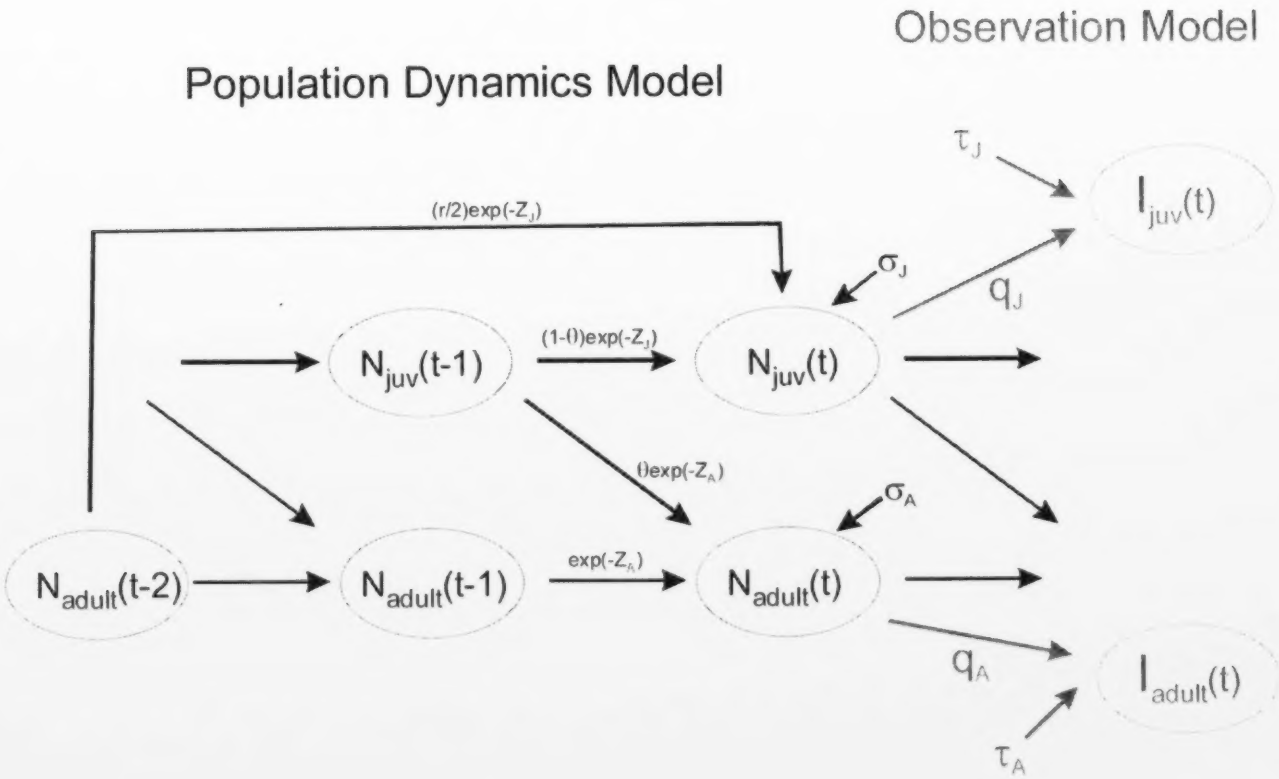


Figure 1. The basic stage-structured state-space model used for winter skate population modeling. *Z* is a mortality rate, *r* is recruitment rate, θ is the transition probability between stages, *q* is catchability, *N* is abundance, *I* is a survey index of abundance, σ is process error, τ is observation error, and *t* indexes time.

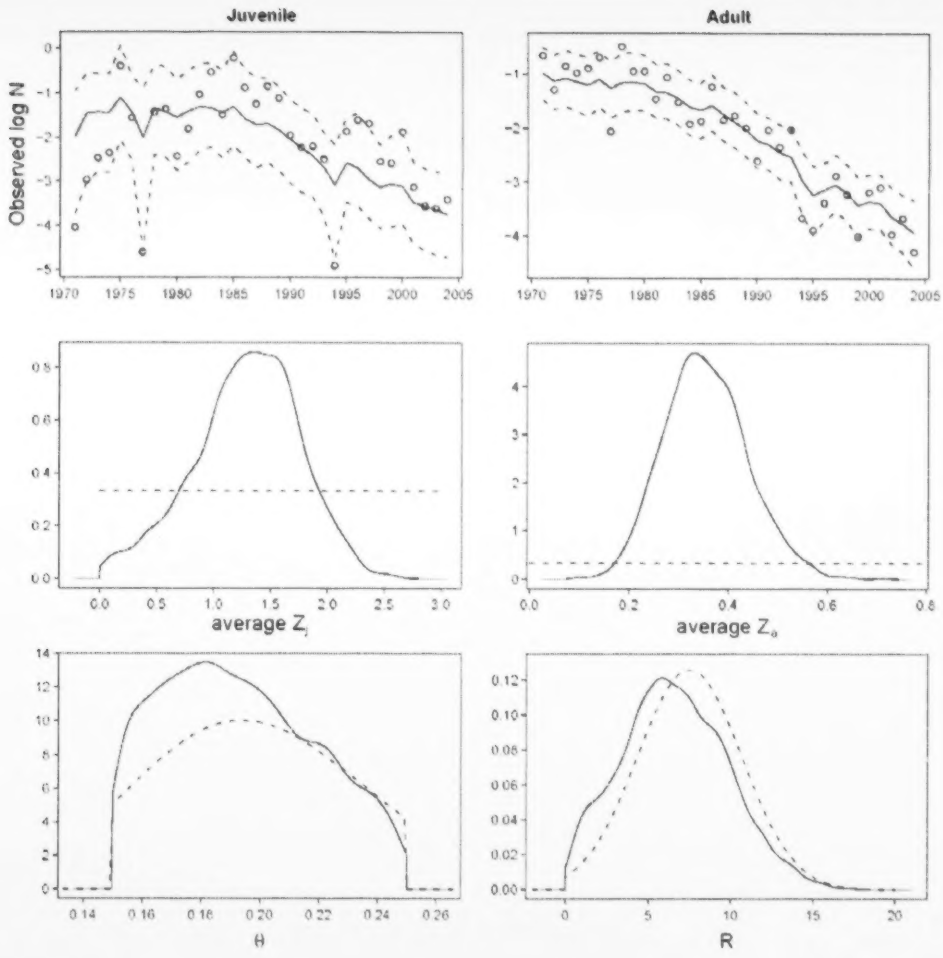


Figure 2. Results for sGSL model Zbar. Upper panels show the observed survey indices (circles) and the median and 95% credible limits of the posterior of the predicted indices (lines). Remaining panels show the prior (dashed line) and posterior (solid line) for selected model parameters.

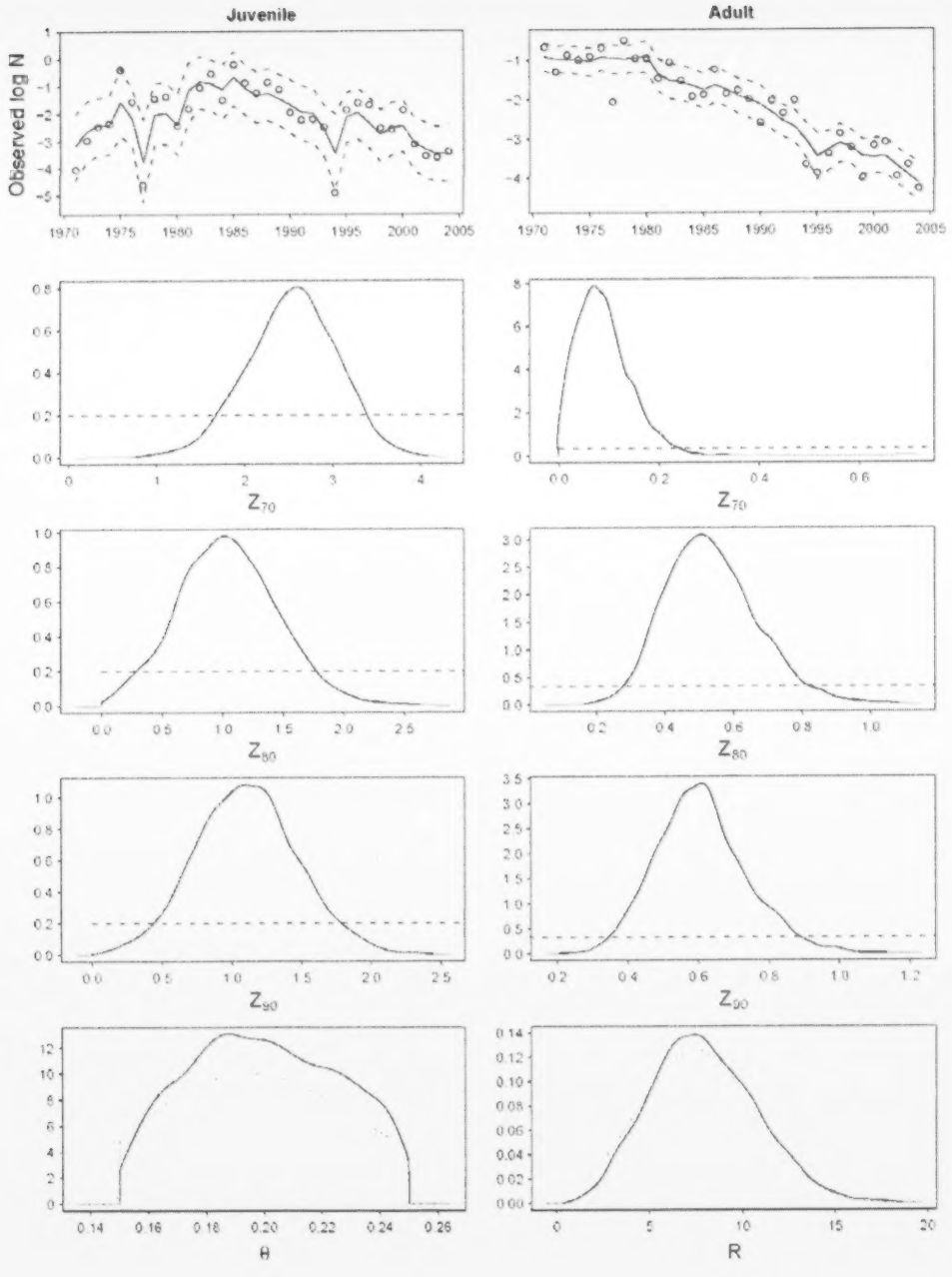


Figure 3. Results for sGSL model Zdec. See Figure 2 caption for details.

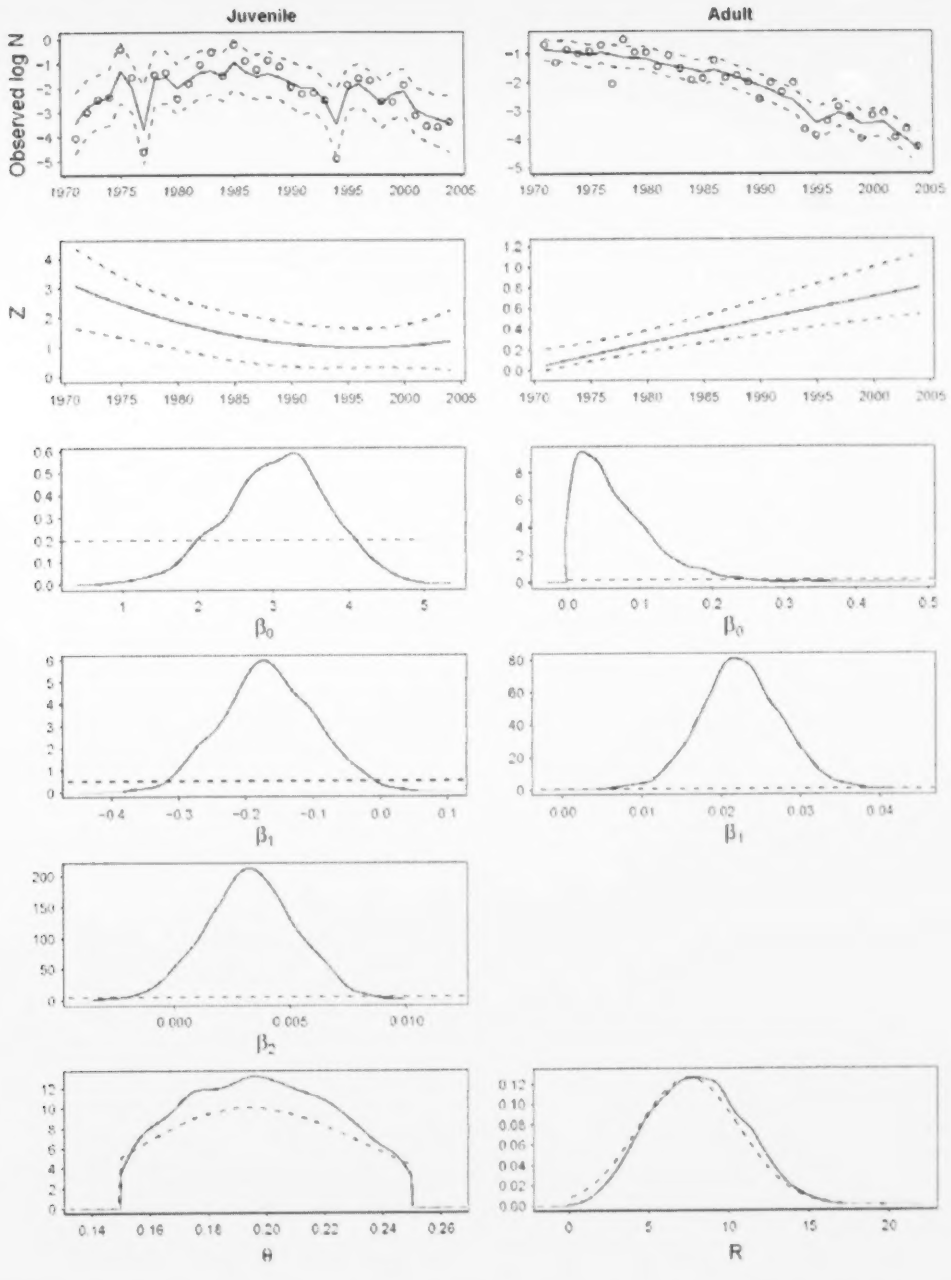


Figure 4. Results for sGSL model with a quadratic trend in juvenile Z and a linear trend in adult Z. Upper panels as in Figure 2. Other panels show the posterior median and 95% credible limits for the Z trends, and the the prior (dashed line) and posterior (solid line) for selected model parameters, including the trend parameters (β's).

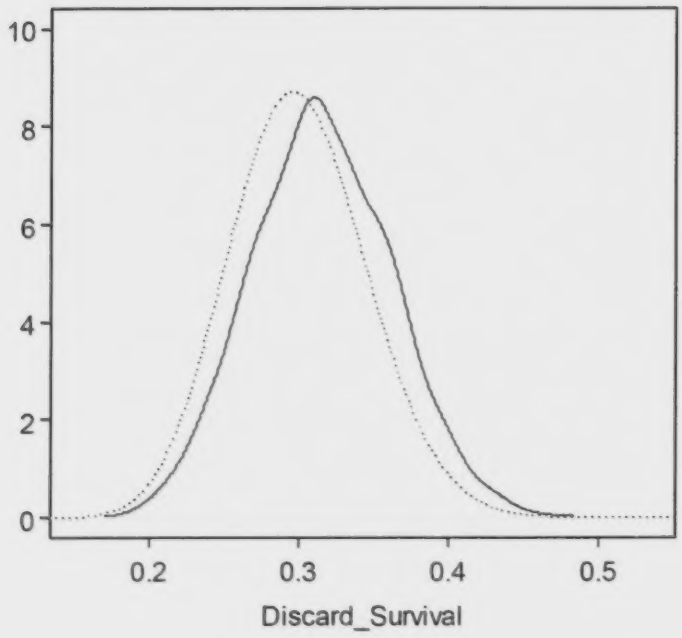


Figure 5. Prior (dashed line) and posterior (solid line) for discard survival in the sGSL Mdec model.

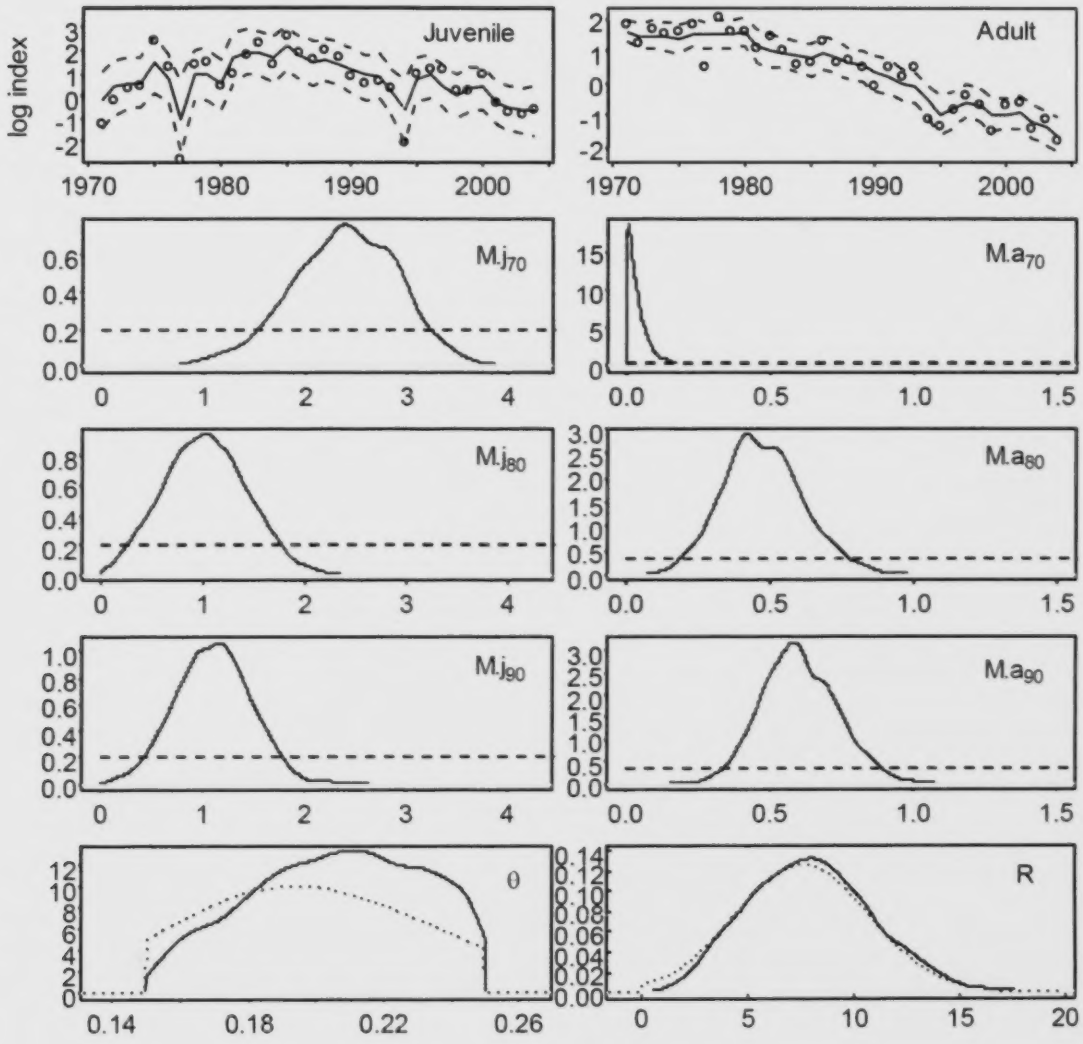


Figure 6. Results for sGSL model Mdec. See Figure 2 caption for details.

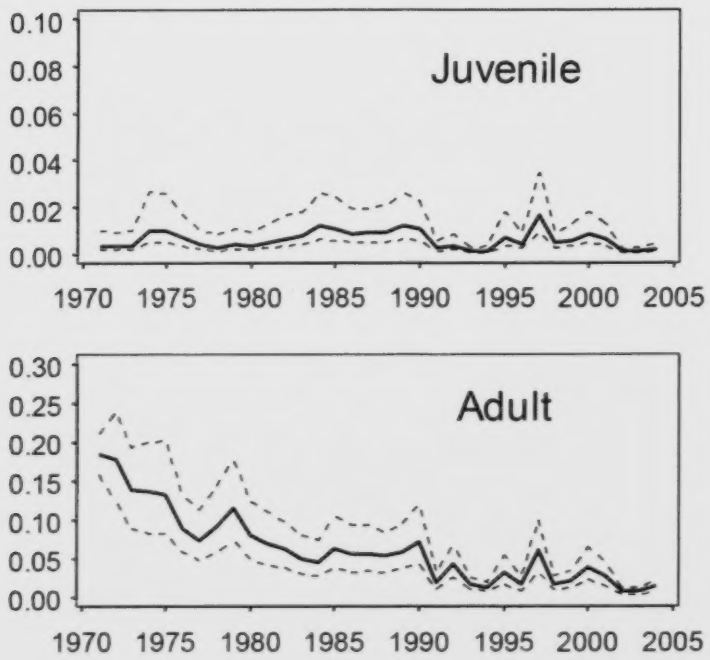


Figure 7. Estimated exploitation rate on juvenile and adult winter skate (median estimate and 95% credible limits) in the southern Gulf of St. Lawrence based on the Mdec model.

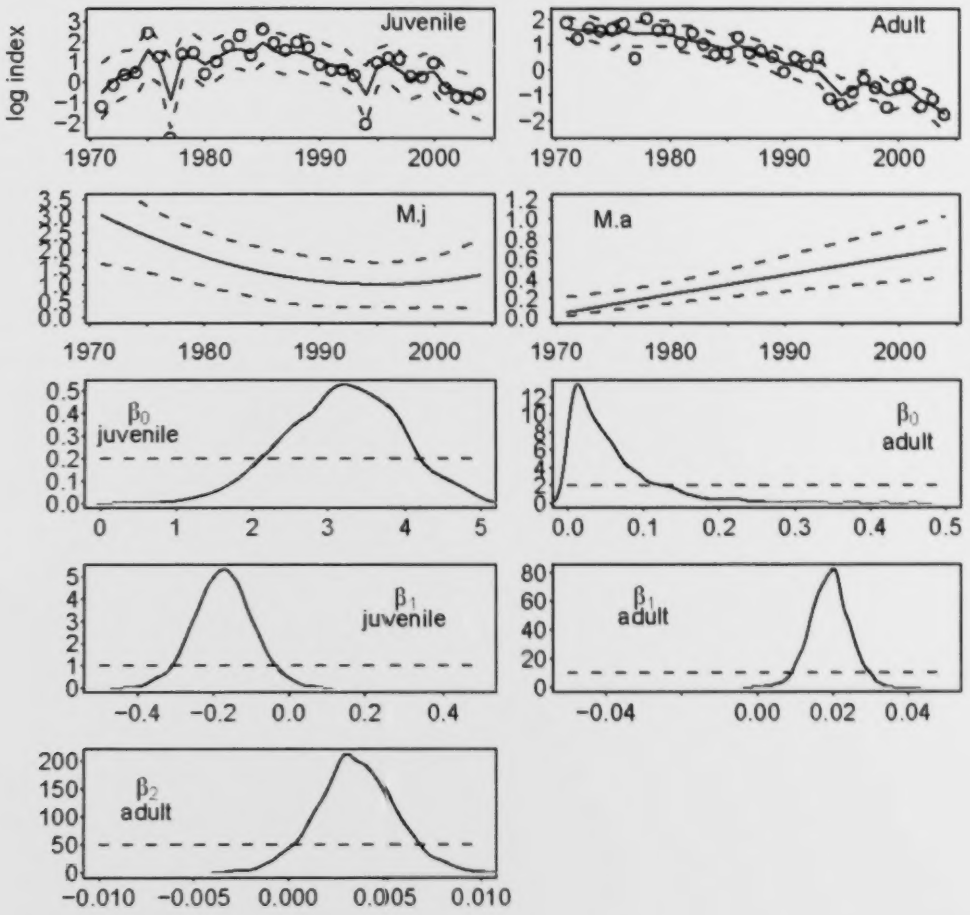


Figure 8. Results for sGSL model with a quadratic trend in juvenile *M* and a linear trend in adult *M*. See Figure 4 caption for details.

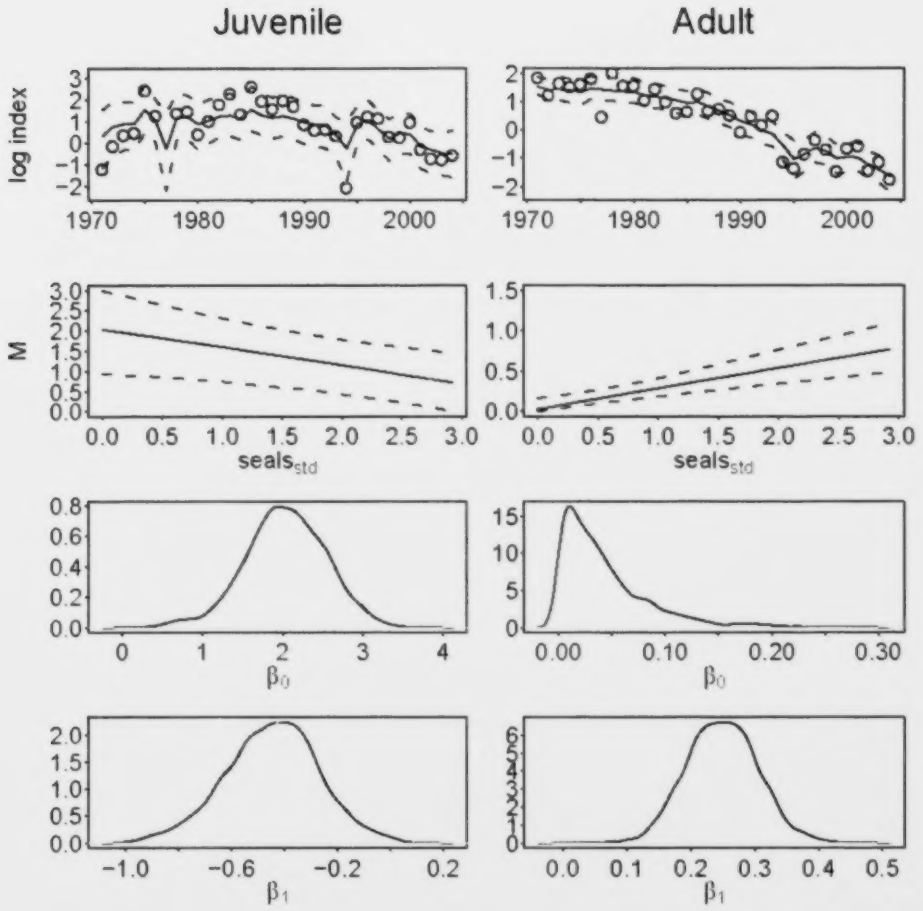


Figure 9. Results for the M-covariate model with both juvenile and adult *M* a function of grey seal abundance. Panels on the left are for juveniles, those on the right for adults.

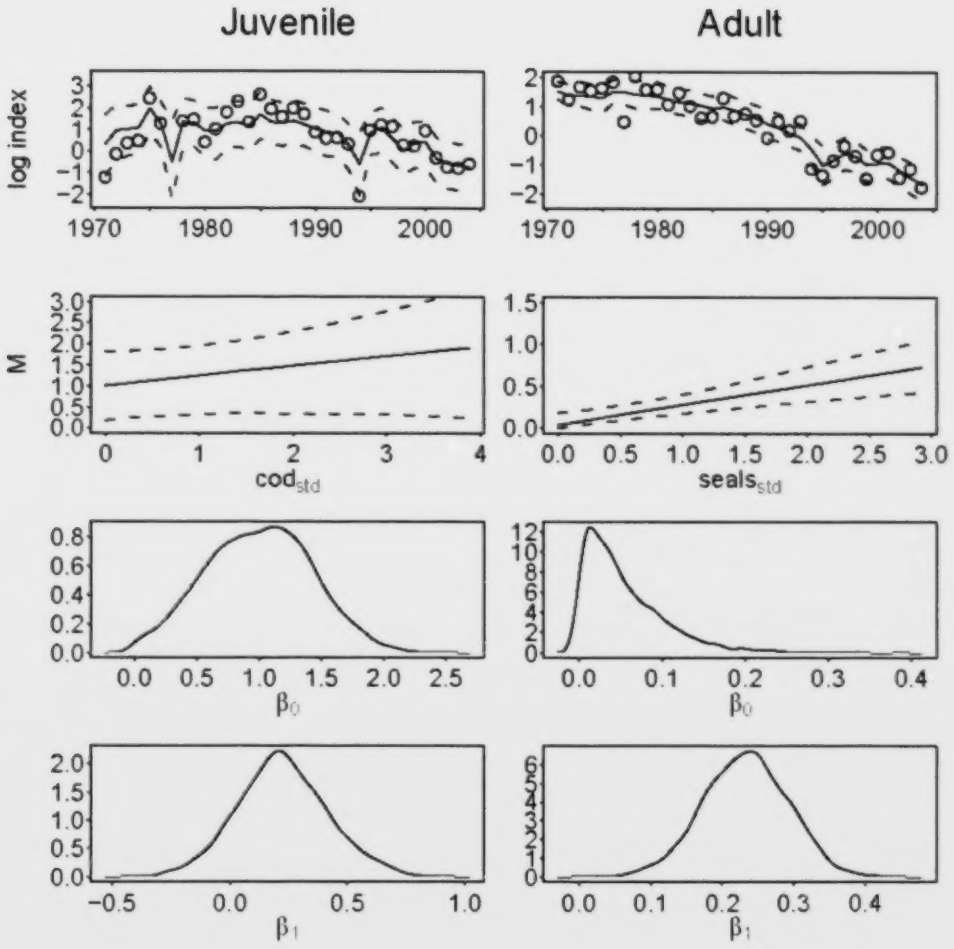


Figure 10. Results for the M-covariate model with adult *M* a function of grey seal abundance and juvenile *M* a function of the abundance of large cod. Panels on the left are for juveniles, those on the right for adults.

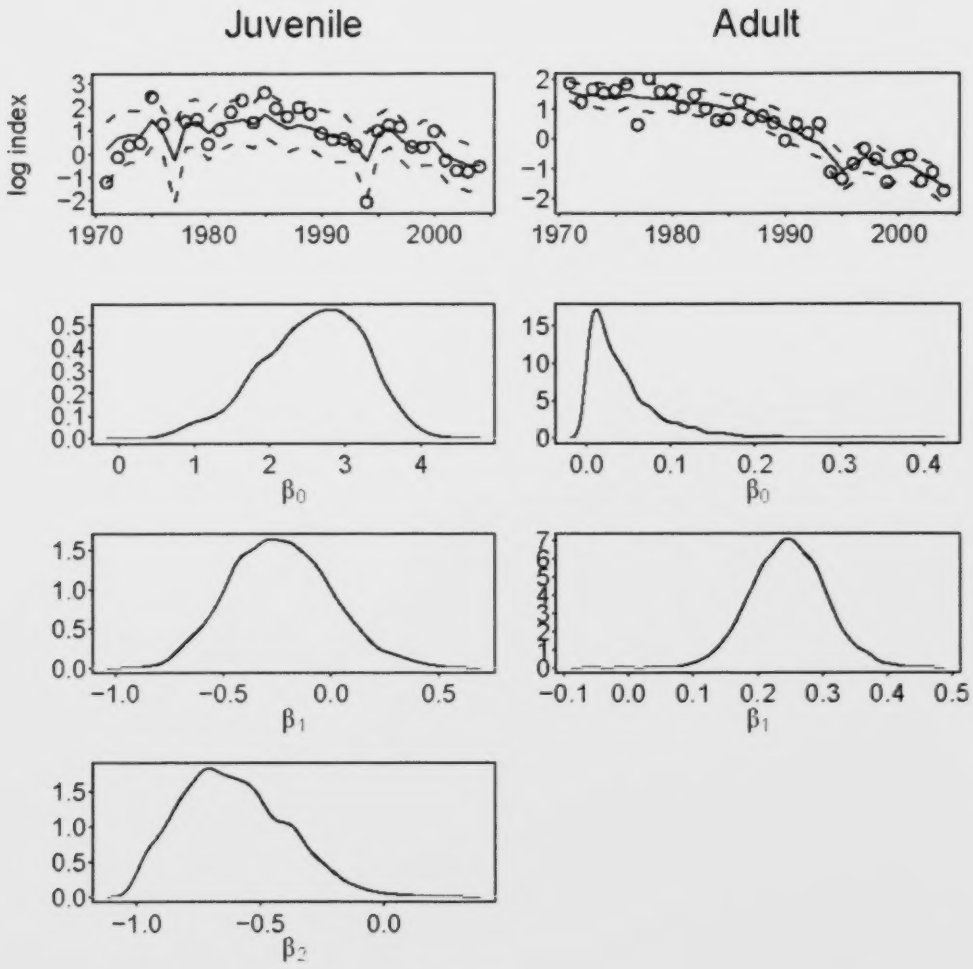


Figure 11. Results for the M-covariate model with adult *M* a function of grey seal abundance and juvenile *M* a function of the abundances of large cod and seals. Panels on the left are for juveniles, those on the right for adults. For juveniles, β_1 is the parameter for the effect of large cod on *M* and β_2 is the parameter for the effect of grey seals.

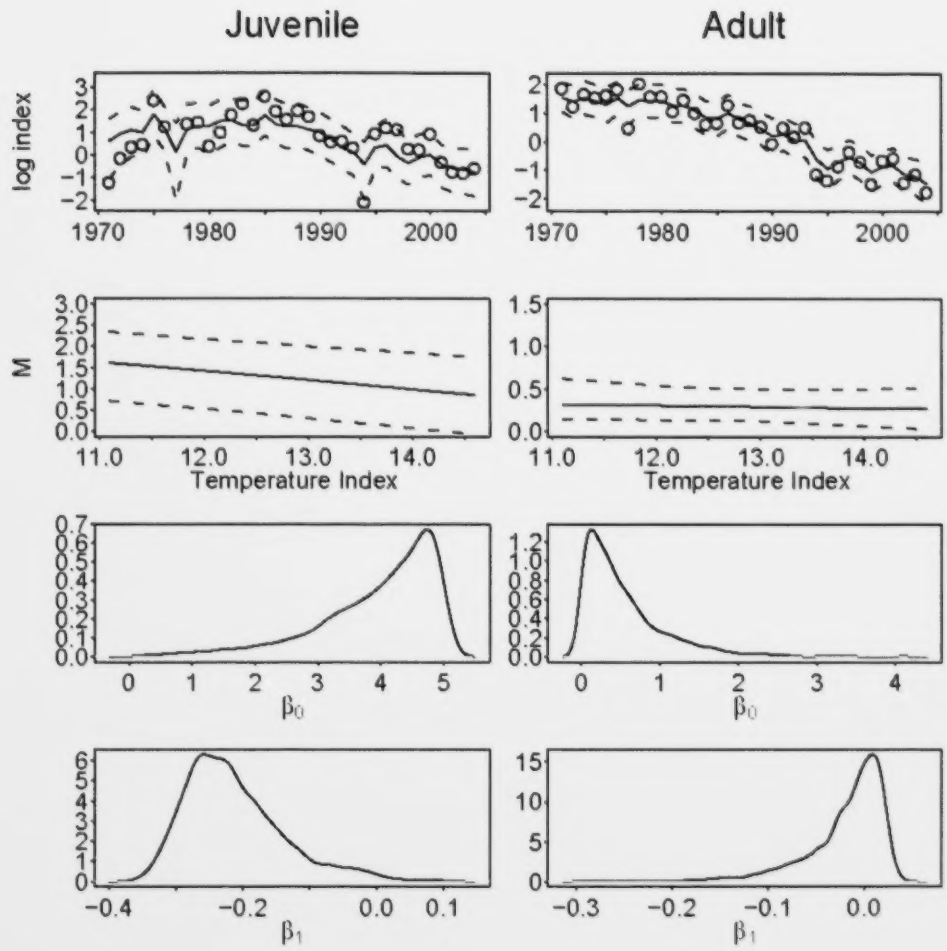


Figure 12. Results for the M-covariate model with both juvenile and adult *M* a function of an inshore temperature index. Panels on the left are for juveniles, those on the right for adults.

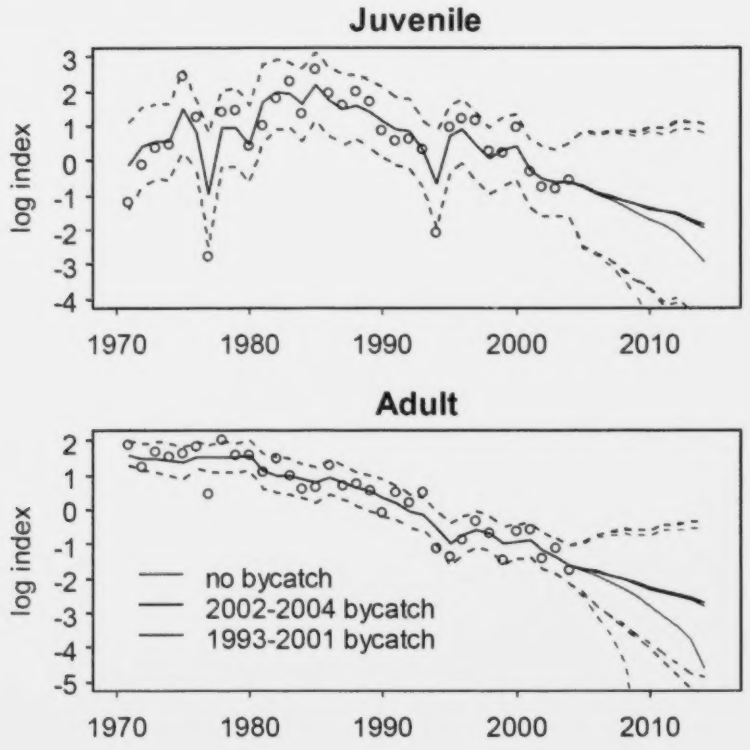


Figure 13. Winter skate abundance in the southern Gulf of St. Lawrence projected 10 years into the future using the Mdec model, given three different bycatch scenarios. Solid lines are the posterior median and dashed lines the 95% credible limits.

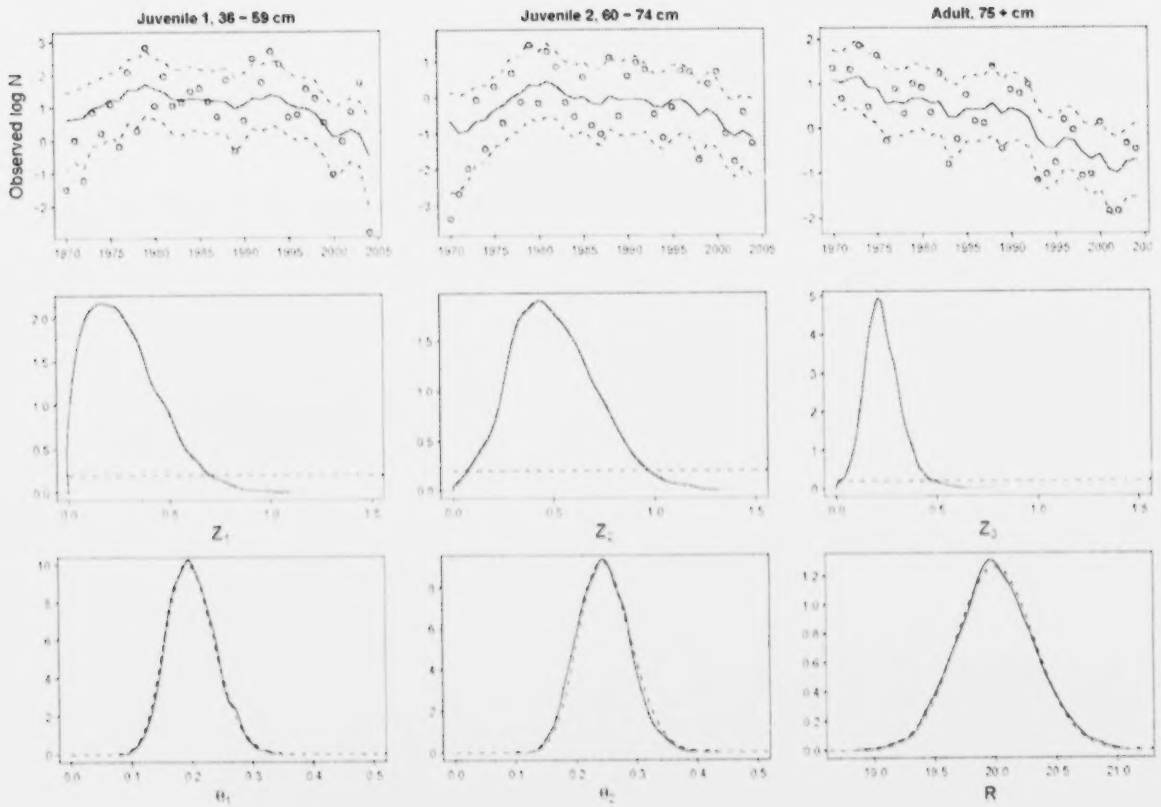


Figure 14. Results of 4VW Zbar model. See Figure 2 caption for details.

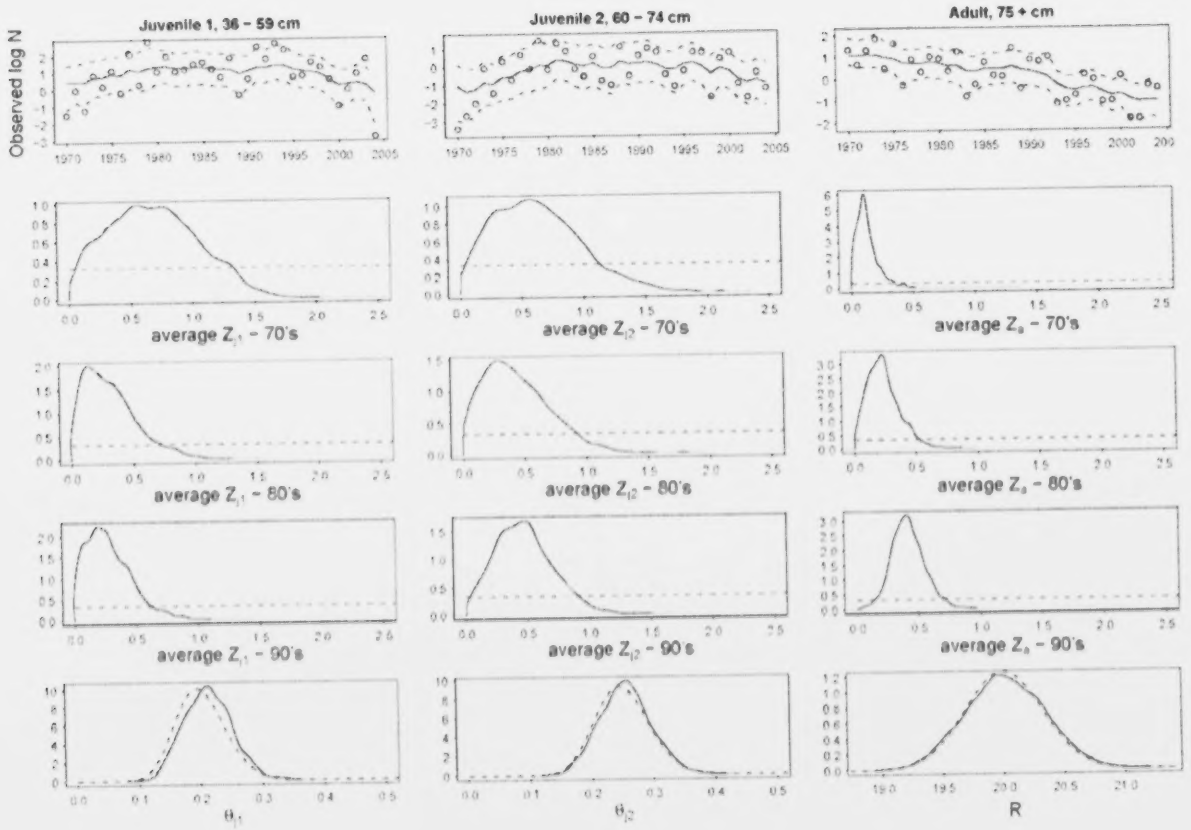


Figure 15. Results for 4VW Zdec model. See caption for Figure 2 for details.

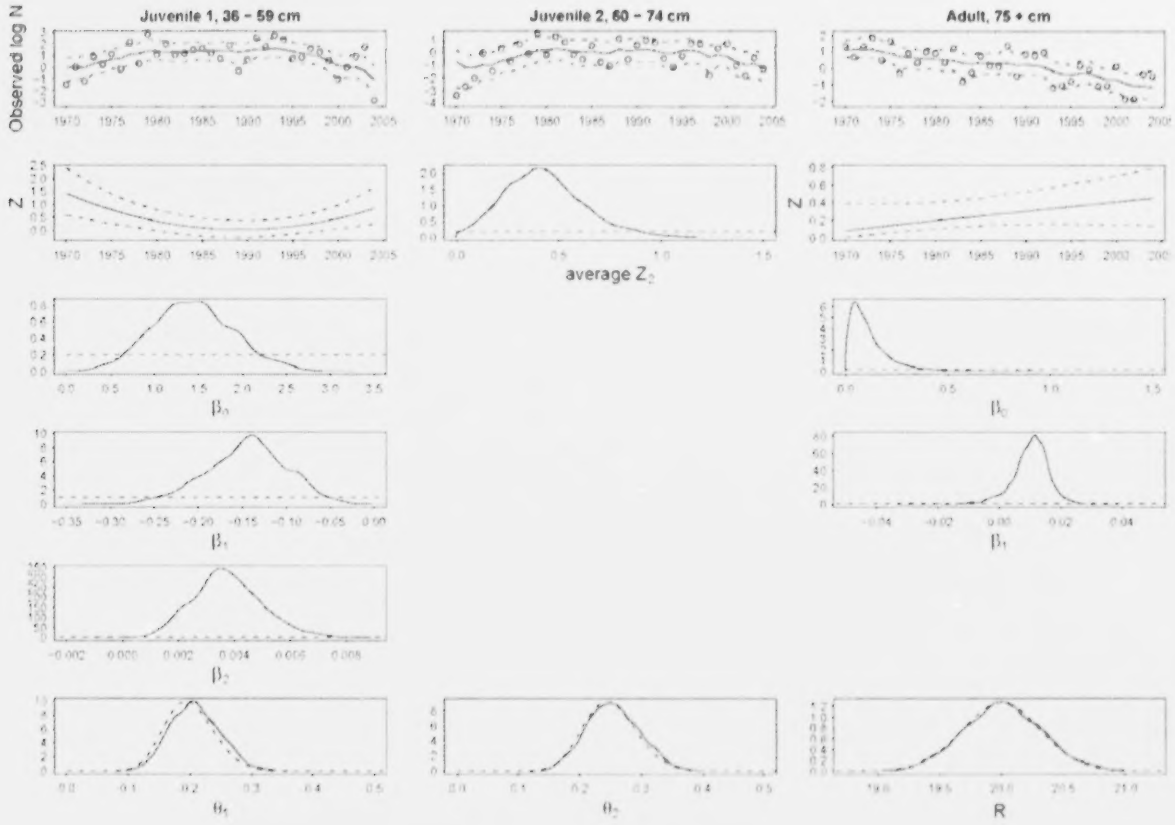


Figure 16. Results for the 4VW Z-trend model. A quadratic trend in Z over time is assumed for the first juvemile stage, constant Z over time is assumed for the second juvenile stage, and a linear trend over time is assumed for the adult stage. See caption to Figure 4 for further details.

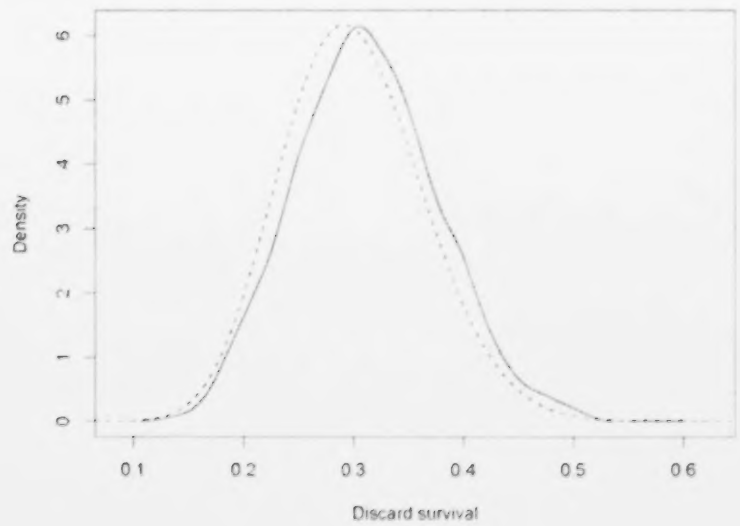


Figure 17. Prior (dashed line) and posterior (solid line) for discard survival in a 4VW M model.

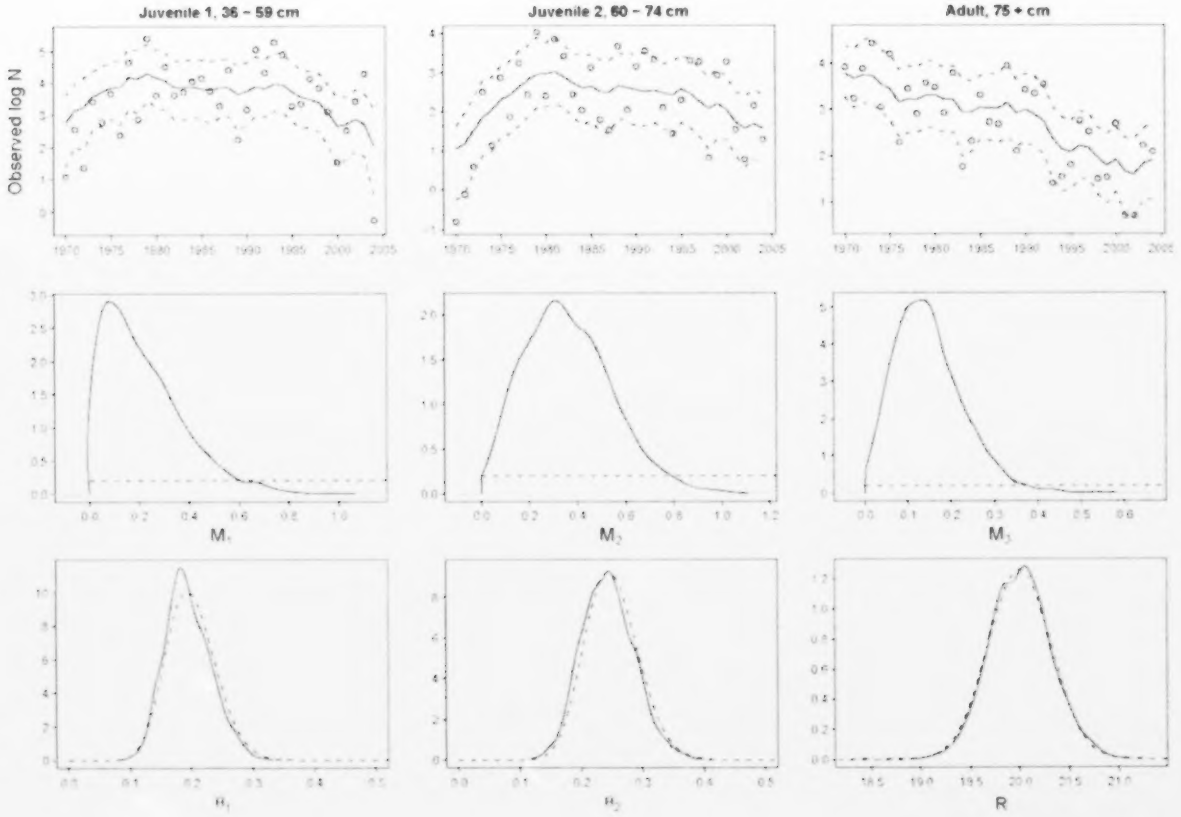


Figure 18. Results for the 4VW Mbar model.

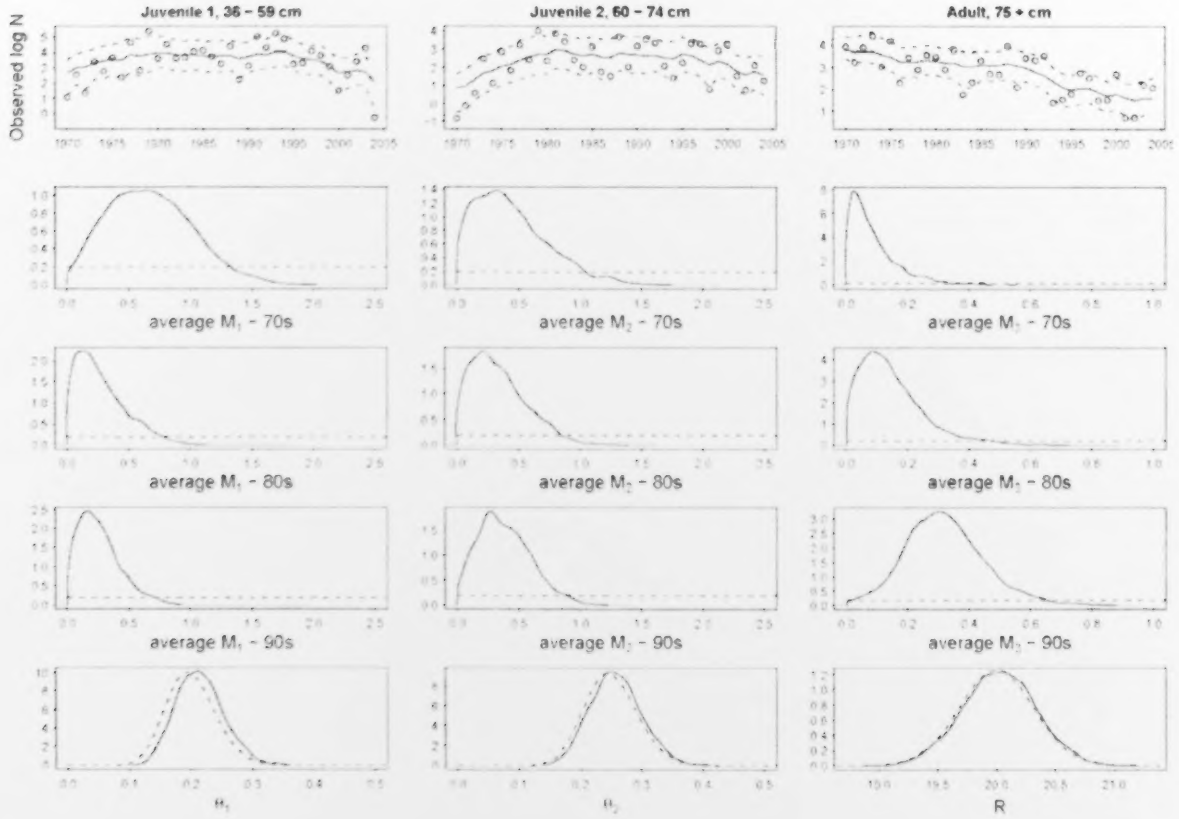

Juvenile 1, 36 – 59 cm
Juvenile 2, 60 – 74 cm
Adult, 75 + cm
Observed log N
average M1 – 70s
average M2 – 70s
average M3 – 70s
average M1 – 80s
average M2 – 80s
average M3 – 80s
average M1 – 90s
average M2 – 90s
average M3 – 90s
R

Figure 19. Results for the 4VW Mdec model.

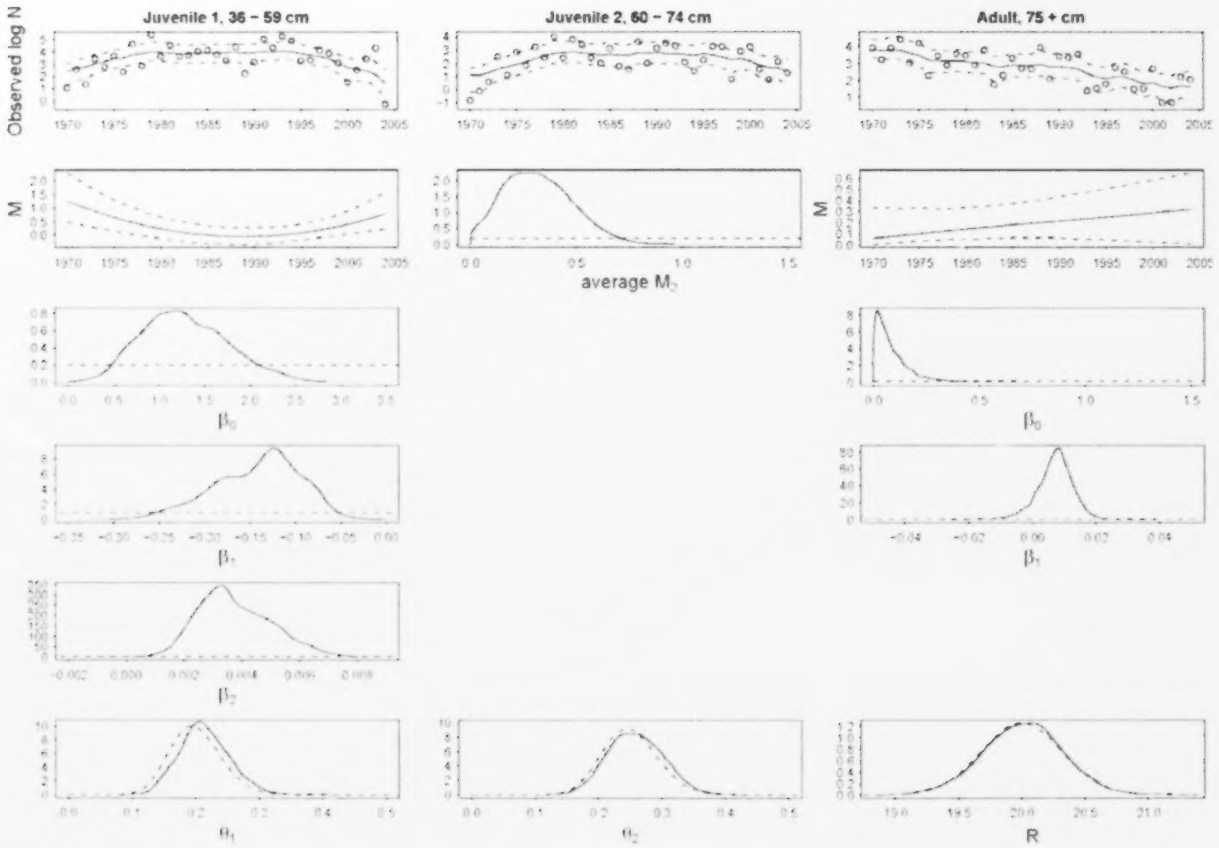


Figure 20. Results for the 4VW M-trend model with a quadratic trend for stage-1 juveniles and a linear trend for adults.

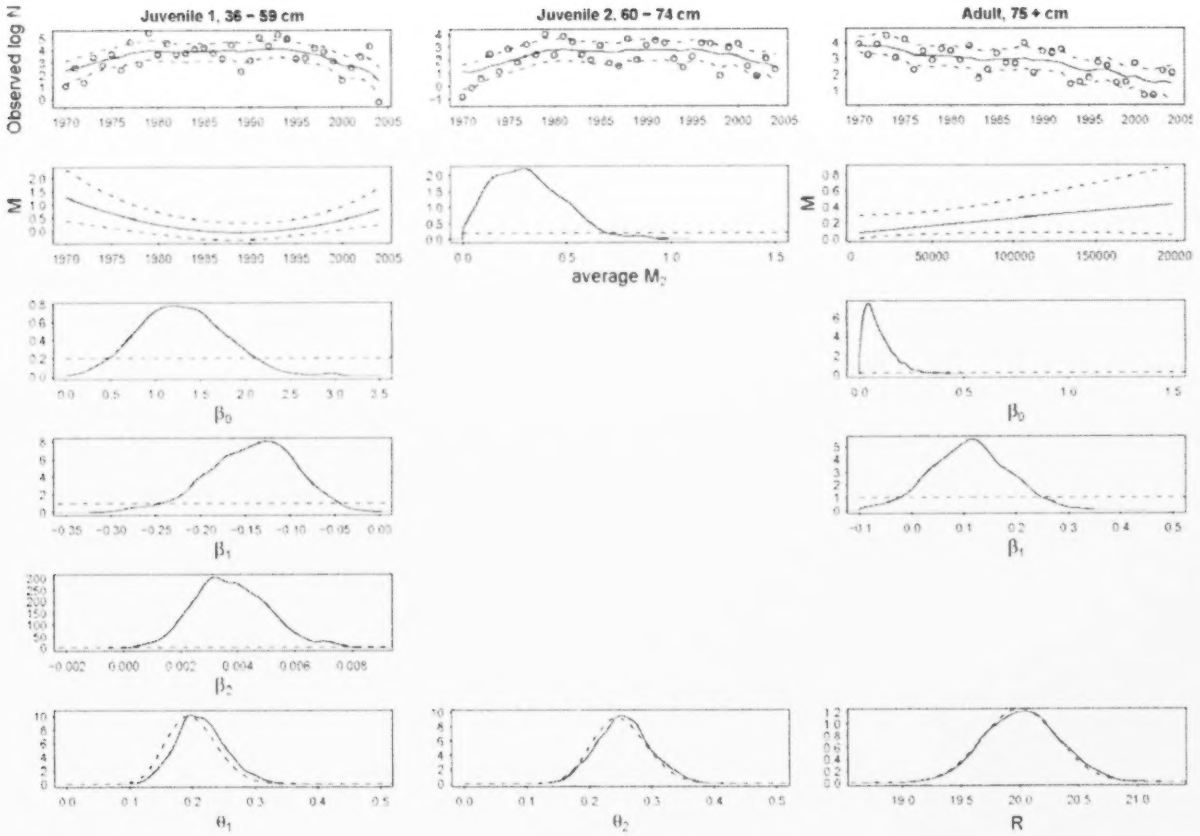


Figure 21. Results for the 4VW M-covariate model with a adult M a function of grey seal abundance.

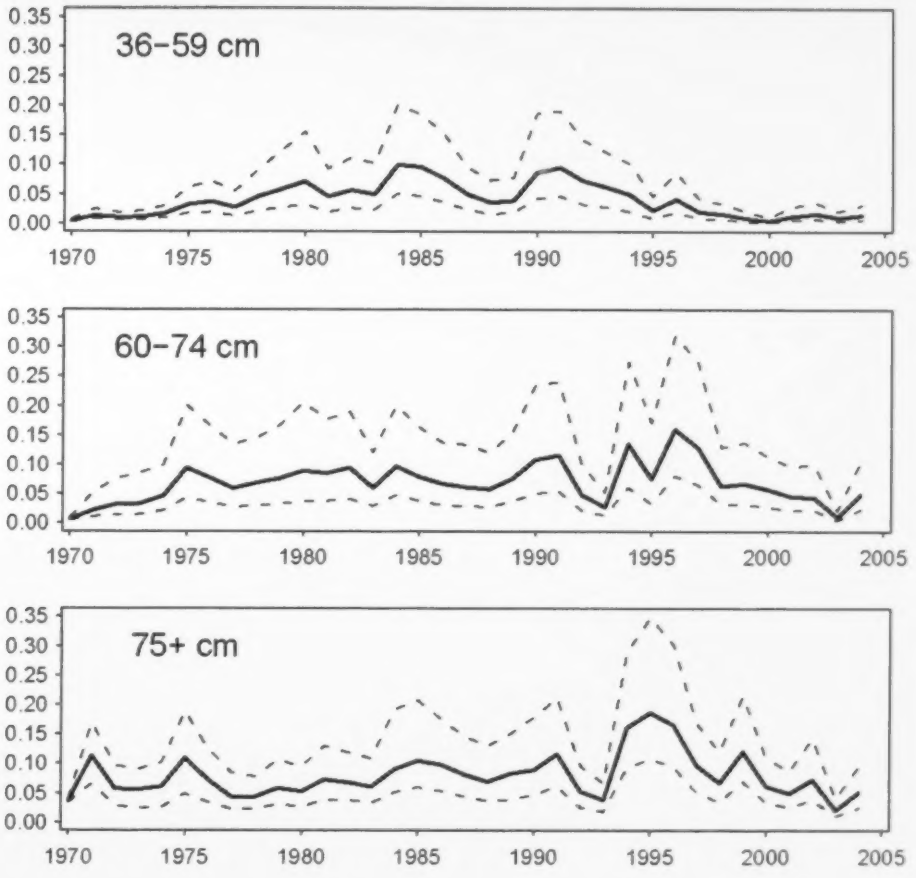


Figure 22. Estimated exploitation rate on juvenile (30-59 cm and 60-74 cm) and adult (75+ cm) winter skate (median estimate and 95% credible limits) in 4VW based on the Mdec model.

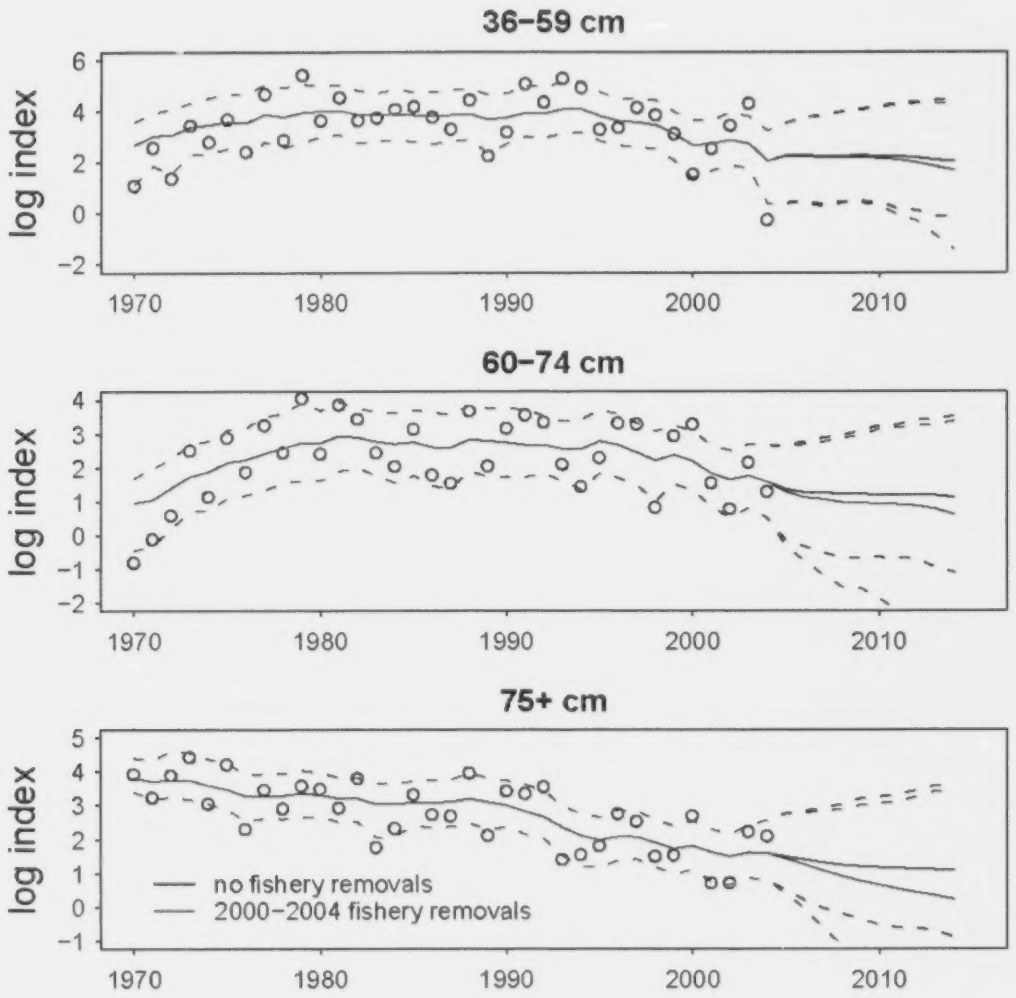


Figure 23. Winter skate abundance in 4VW projected 10 years into the future using the Mdec model, given two different bycatch scenarios. Solid lines are the posterior median and dashed lines the 95% credible limits.

Appendix A: WinBUGS model for the southern Gulf of St. Lawrence population allowing decadal variation in total mortality of juveniles and adults

```
model;
{
# dps - decadal mortality model

# Informative Priors equivalent to q=1 (1/trawlable_units)
#sd=0.1
q.j ~ dnorm(0.7, 100)I(0, )
q.a ~ dnorm(1, 100)I(0, )

# Observation error variance
sdobs.j ~ dunif(0.6, 1.2)
sdobs.a ~ dunif(0.4, 0.8)

itau2.j <- pow(sdobs.j, -2)
itau2.a <- pow(sdobs.a, -2)

# Priors for translation probabilities
theta ~ dbeta(20, 80)I(0.15, 0.25)

# Priors for instantaneous mortality rates
z.j[1] ~ dunif(0, 5)
z.a[1] ~ dunif(0, 3)
z.j[2] ~ dunif(0, 5)
z.a[2] ~ dunif(0, 3)
z.j[3] ~ dunif(0, 5)
z.a[3] ~ dunif(0, 3)

for (i in 1:3) {
        s.j[i] <- exp(-z.j[i])
        s.a[i] <- exp(-z.a[i])
        }

# Priors for recruitment rate
recrate ~ dnorm(7.5, 0.1)I(0, )

#non-informative prior for process error
sdpro.j ~ dunif(0, 1)
sdpro.a ~ dunif(0, 1)
isigma2.j <- pow(sdpro.j, -2)
isigma2.a <- pow(sdpro.a, -2)

# Informative Priors for inital abundance (based on survey indices in the 1970s)
# sd=20
Nad69 ~ dnorm(0.4, 100)I(0, )
Nad70 ~ dnorm(0.4, 100)I(0, )
Njuv70 ~ dnorm(0.1, 100)I(0, )

# Process equation
for (t in 1:10) {
        sjuve[t] <- exp(-z.j[1])
        smat[t] <- exp(-z.a[1])
        }
for (t in 11:20) {
        sjuve[t] <- exp(-z.j[2])
        smat[t]<-exp(-z.a[2])
        }
for (t in 21:34) {
        sjuve[t] <- exp(-z.j[3])
        smat[t] <- exp(-z.a[3])
        }

n.j[1] <- log((Njuv70 * (1 - theta) + Nad69 * recrate / 2) * sjuve[1])
n.a[1] <- log((Nad70 + Njuv70 * theta) * smat[1])
```

```
N.j[1] ~ dlnorm(n.j[1], isigma2.j)
N.a[1] ~ dlnorm(n.a[1], isigma2.a)

n.j[2] <- log((N.j[1] * (1 - theta) + Nad70 * recrate / 2) * sjuve[2])
n.a[2] <- log((N.a[1] + N.j[1] * theta) * smat[2])
N.j[2] ~ dlnorm(n.j[2], isigma2.j)
N.a[2] ~ dlnorm(n.a[2], isigma2.a)

for (t in 3:34) {
        n.j[t] <- log((N.j[t-1] * (1 - theta) + N.a[t-2] * recrate / 2) * sjuve[t])
        n.a[t] <- log((N.a[t-1] + N.j[t-1] * theta) * smat[t])
        N.j[t] ~ dlnorm(n.j[t], isigma2.j)
        N.a[t] ~ dlnorm(n.a[t], isigma2.a)
        }

# Observation equation

for (t in 1:34)  {
        logind.j[t] <- log(q.j * N.j[t])
        logind.a[t] <- log(q.a * N.a[t])

        obs.j[t] ~ dlnorm(logind.j[t], itau2.j)
        obs.a[t] ~ dlnorm(logind.a[t], itau2.a)
        }
}
```

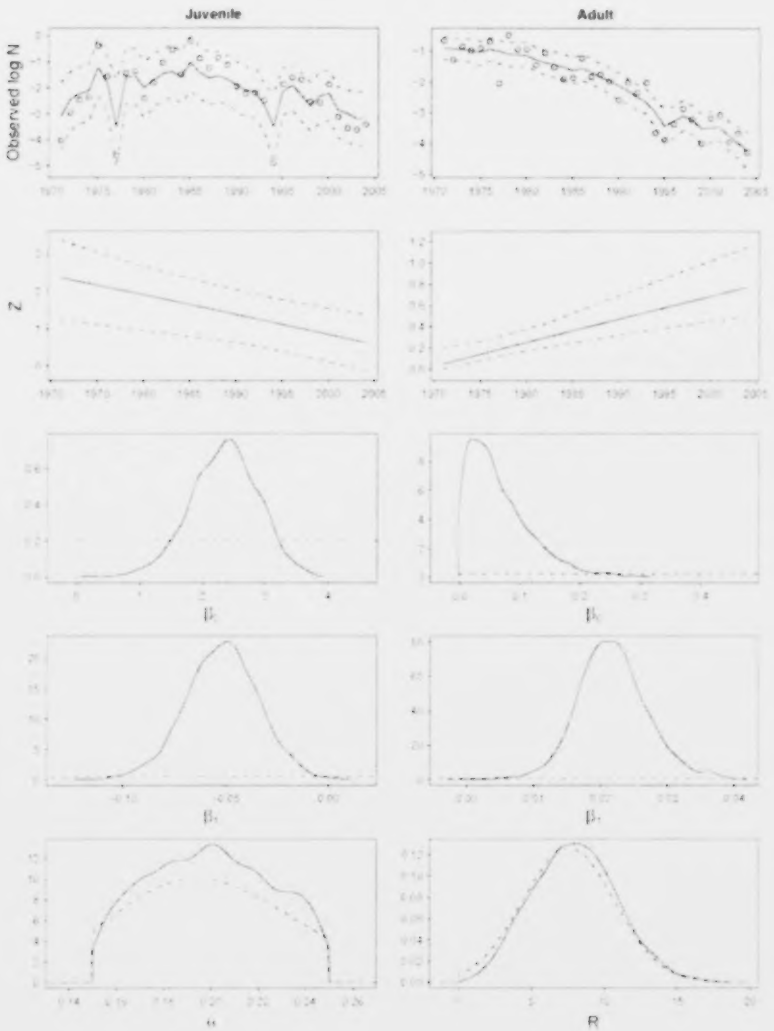
Appendix B: WinBUGS model for the southern Gulf of St. Lawrence population including fishery removals (discards) and allowing decadal variation in natural mortality of juveniles and adults

```
model;
{
# dps - decadal mortality model

eps <- 0.0001

# Informative Priors equivalent to q=1 (1/trawlable_units)
#sd=0.1
q.j ~ dnorm(1, 100)I(0, )
q.a ~ dnorm(1, 100)I(0, )

# Observation error variance
sdobs.j ~ dunif(0.6, 1.2)
sdobs.a ~ dunif(0.4, 0.8)
itau2.j <- pow(sdobs.j, -2)
itau2.a <- pow(sdobs.a, -2)

# Priors for transistion probabilities
theta ~ dbeta(20, 80)I(0.15, 0.25)

# Prior for discard survival rate (peak at 0.3)
d.surv ~ dbeta(30, 70)

# Priors for instantaneous mortality rates
m.j[1] ~ dunif(0, 5)
m.a[1] ~ dunif(0, 3)
m.j[2] ~ dunif(0, 5)
m.a[2] ~ dunif(0, 3)
m.j[3] ~ dunif(0, 5)
m.a[3] ~ dunif(0, 3)

# Priors for recruitment rate
recrate ~ dnorm(7.5, 0.1)I(0, )

#non-informative prior for process error
sdpro.j ~ dunif(0, 1)
sdpro.a ~ dunif(0, 1)
isigma2.j <- pow(sdpro.j, -2)
isigma2.a <- pow(sdpro.a, -2)

# Informative Priors for inital abundance (based on survey catch rates in the 1970s)
# sd=20
Nad69 ~ dnorm(5.0, 100)I(0, )
Nad70 ~ dnorm(5.0, 100)I(0, )
Njuv70 ~ dnorm(1.5, 100)I(0, )

# Process equation
for (i in 1:34) {
 c.j[i] <- (1 - d.surv) * disc.j[i]
 c.a[i] <- (1 - d.surv) * disc.a[i]
}

for (t in 1:10) {
        sjuve[t] <- exp(-m.j[1])
        smat[t] <- exp(-m.a[1])
        }
for (t in 11:20) {
        sjuve[t] <- exp(-m.j[2])
        smat[t]<-exp(-m.a[2])
        }
for (t in 21:34) {
        sjuve[t] <- exp(-m.j[3])
        smat[t] <- exp(-m.a[3])
        }
```

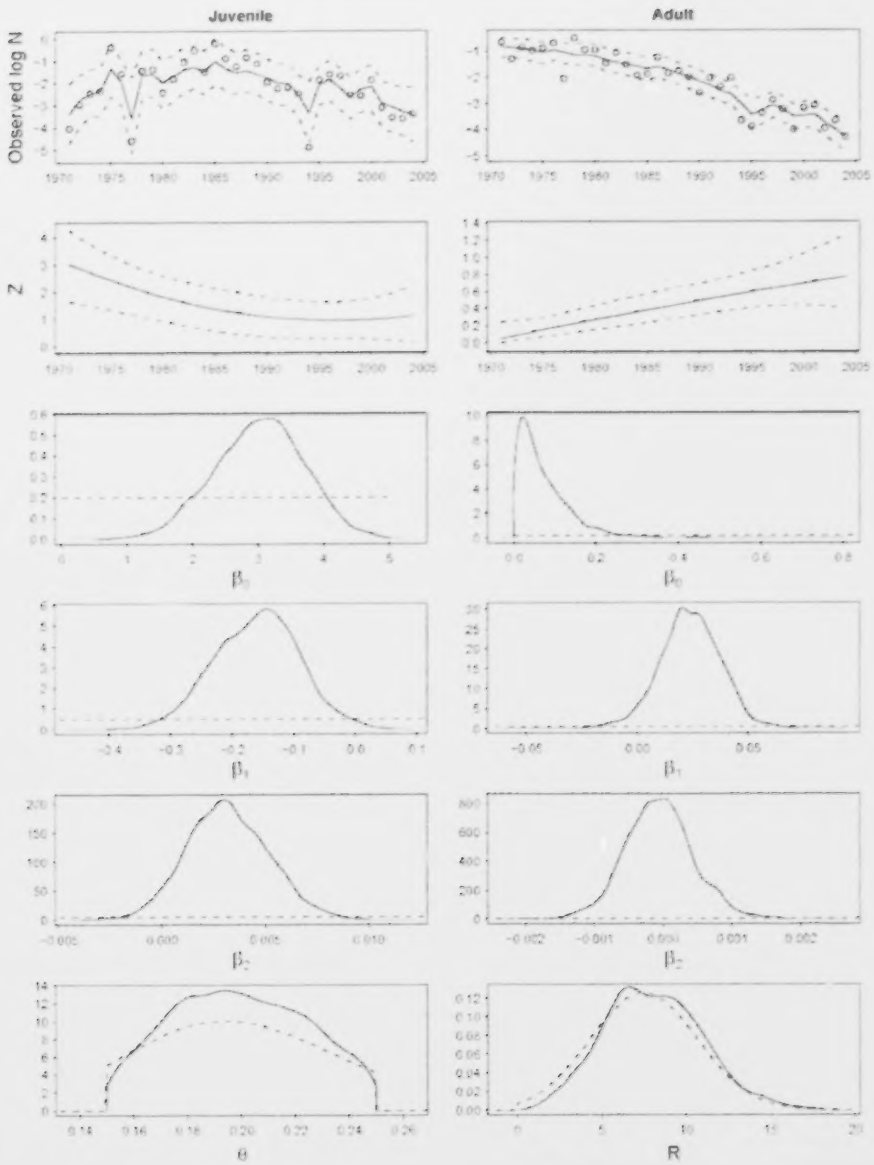
```
tmp.j[1] <- Njuv70 * (1 - theta) + Nad69 * recrate / 2
exploit.j[1] <- c.j[1] / tmp.j[1]
n.j[1] <- log(tmp.j[1] * max(1 - exploit.j[1], eps) * sjuve[1])
N.j[1] ~ dlnorm(n.j[1], isigma2.j)
z.j[1] <- -log((1 - exploit.j[1])^sjuve[1])

tmp.a[1] <- Nad70 + Njuv70 * theta
exploit.a[1] <- c.a[1] / tmp.a[1]
n.a[1] <- log(tmp.a[1] * max(1 - exploit.a[1], eps) * smat[1])
N.a[1] ~ dlnorm(n.a[1], isigma2.a)
z.a[1] <- -log((1 - exploit.a[1])^smat[1])

tmp.j[2] <- N.j[1] * (1 - theta) + Nad70 * recrate / 2
exploit.j[2] <- c.j[2] / tmp.j[2]
n.j[2] <- log(tmp.j[2] * max(1 - exploit.j[2], eps) * sjuve[2])
N.j[2] ~ dlnorm(n.j[2], isigma2.j)
z.j[2] <- -log((1 - exploit.j[2])^sjuve[2])

tmp.a[2] <- N.a[1] + N.j[1] * theta
exploit.a[2] <- c.a[2] / tmp.a[2]
n.a[2] <- log(tmp.a[2] * max(1 - exploit.a[2], eps) *smat[2])
N.a[2] ~ dlnorm(n.a[2], isigma2.a)
z.a[2] <- -log((1 - exploit.a[2])^smat[2])

for (t in 3:34) {
        tmp.j[t] <- N.j[t-1] * (1 - theta) + N.a[t-2] * recrate / 2
        exploit.j[t] <- c.j[t] / tmp.j[t]
        n.j[t] <- log(tmp.j[t] * max(1 - exploit.j[t], eps) * sjuve[t])
        N.j[t] ~ dlnorm(n.j[t], isigma2.j)
        z.j[t] <- -log((1 - exploit.j[t])^sjuve[t])

        tmp.a[t] <- N.a[t-1] + N.j[t-1] * theta
        exploit.a[t] <- c.a[t] / tmp.a[t]
        n.a[t] <- log(tmp.a[t] * max(1 - exploit.a[t], eps) * smat[t])
        N.a[t] ~ dlnorm(n.a[t], isigma2.a)
        z.a[t] <- -log((1 - exploit.a[t])^smat[t])
        }

# Observation equation

for (t in 1:34)  {
        logind.j[t] <- log(q.j * N.j[t])
        logind.a[t] <- log(q.a * N.a[t])
        obs.j[t] ~ dlnorm(logind.j[t], itau2.j)
        obs.a[t] ~ dlnorm(logind.a[t], itau2.a)
        }
}
```

Appendix C: Results for additional southern Gulf of St. Lawrence *Z-trend* models
(see captions to Figures 2-4 for details)

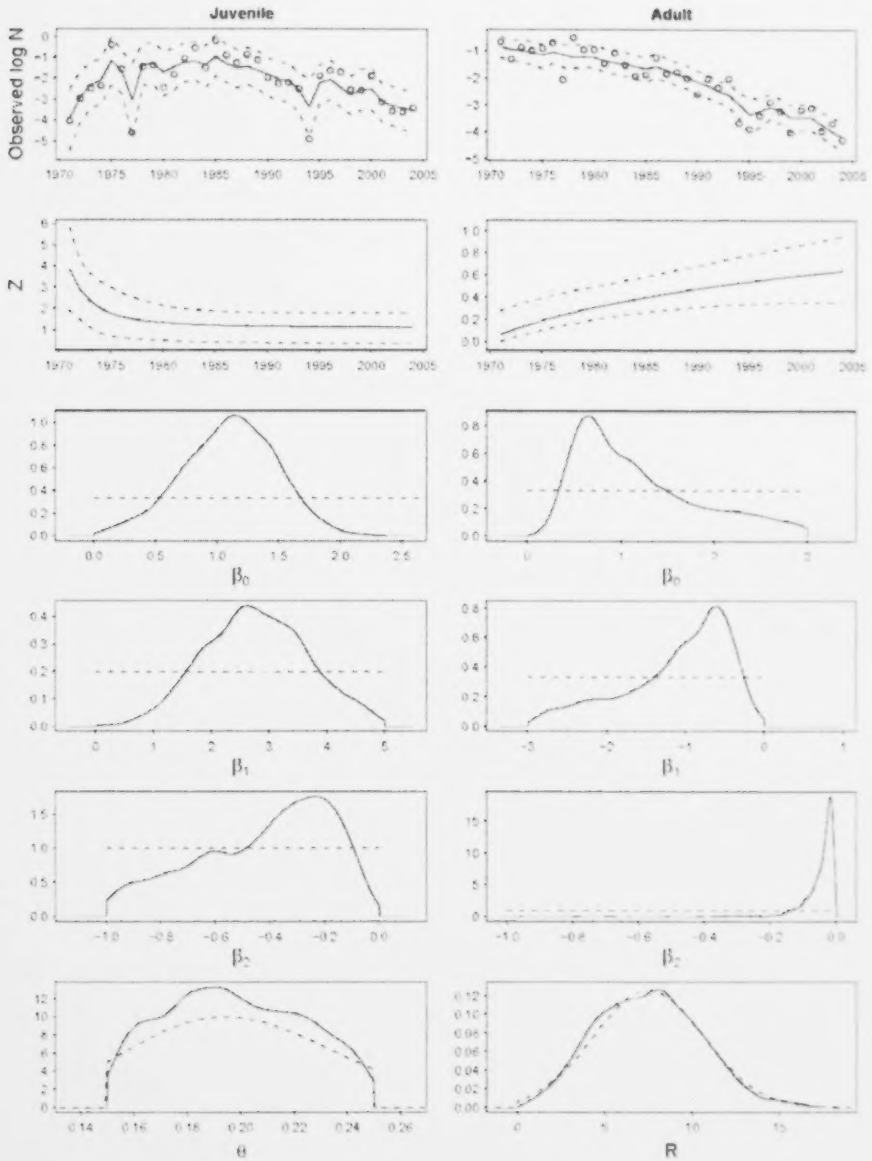
1. Linear trends in juvenile and adult mortality



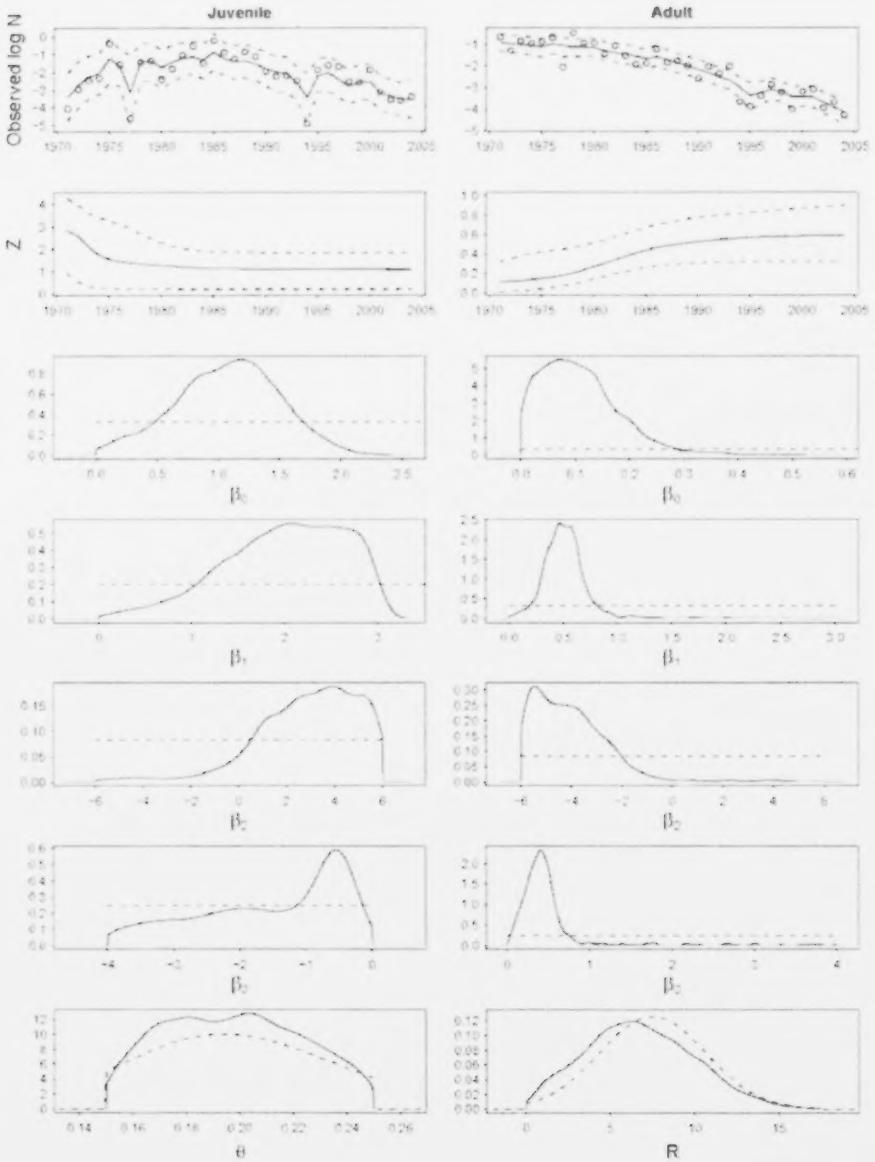
2. Quadratic trends in juvenile and adult mortality



3. Asymptotic trends in juvenile and adult mortality



4. Sigmoid trends in juvenile and adult mortality



5. Asymptotic trend in juvenile and linear trend in adult mortality